ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF LOCOMOTOR PERFORMANCE IN COLLARED LIZARDS (*CROTAPHYTUS COLLARIS*)

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SIGNIFICANCE OF LOCOMOTOR PERFORMANCE

IN COLLARED LIZARDS

(*CROTAPHYTUS COLLARIS*)

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INTRODUCTION

This project was designed to test several hypotheses concerning the evolution of locomotor performance in collared lizards, specifically examining the roles of natural and sexual selection and differences between the sexes during ontogeny. This research is presented as a series of papers in correct format for submission to an appropriate scientific journal. Chapter 2 is in correct format for submission to *Evolution*, chapter 3 for *Functional Ecology*, chapter 4 for *Functional Ecology*, and chapter 5 for *Evolution*.

FIELD USE OF MAXIMAL SPRINT SPEED BY COLLARED LIZARDS (*CROTAPHYTUS COLLARIS*): SEXUAL SELECTION AND COMPENSATION

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***Abstract.* –** To understand how selection acts on performance capacity, the ecological role of the performance parameter being measured must be determined. Knowing if and when an animal uses maximal performance capacity may give insight into what specific selective pressures may be acting upon morphology and performance, because individuals are expected to use close to maximal capacity only in contexts involving an important selective force. Further, if a selective force is important, poor performers are expected to behaviorally compensate. To understand the relative roles of natural and sexual selection on maximal sprint speed capacity I measured maximal sprint speed of collared lizards (*Crotaphytus collaris*) in the laboratory and field-realized sprint speed for the same individuals in three different contexts (foraging, escaping a predator, and responding to a rival intruder). Females used closer to maximal speed while escaping predators than in the other contexts. Adult males, on the other hand, used closer to maximal speed while responding to an unfamiliar male intruder tethered within their territory. Sprint speeds during foraging attempts were far below maximal capacity for all lizards. Yearlings appeared to compensate for having lower absolute maximal capacity by using a greater percentage of their maximal capacity while foraging and escaping

predators than adults of either sex did. I also found evidence for compensation within age and sex classes, where slower individuals used a greater percentage of their maximal capacity than faster individuals. However, this was true only while foraging and escaping predators, and not while responding to a rival. Collared lizards appeared to choose microhabitats near refugia such that maximal speed was not necessary to escape predators. Although natural selection for predator avoidance cannot be ruled out as a strong selective force acting on locomotor performance in collared lizards, especially in females, intrasexual selection for territory maintenance may be a stronger selective agent in males.

INTRODUCTION

Individual variation in fitness reflects variation in underlying morphological and physiological traits, but it is generally accepted that this relationship is mediated by whole-animal performance (Huey and Stevenson 1979; Arnold 1983). Arnold's (1983) formalized operational framework for linking morphology, performance, and fitness has been extended and refined by many authors (e.g., Bennett and Huey 1990; Wainwright and Reilly 1994; Irschick and Garland 2001; Irschick 2002), most importantly by adding behavior as a filter between performance and fitness (Garland and Losos 1994; Irschick and Garland 2001). Only by knowing how organisms utilize maximal performance in nature can we understand how selection may be acting on those performance traits. Quantifying the use of maximal performance capacity in various ecological contexts in nature (i.e., "ecological performance," Irschick 2003) can give greater insight into selective pressures than can be gained from studies of only correlation between performance and fitness may not reveal. Studying performance in nature provides two

useful datasets when paired with maximal capacity data: (1) one can calculate percentage of maximal capacity used in various contexts and (2) one can determine if there is compensation by poor performers. Further an ecological context is likely to be an important selective factor if, in that context: (1) percentage of maximal capacity used is high, (2) compensation is present, and (3) individuals with a higher maximal capacity perform at a higher level than worse performers.

Irschick and Garland (2001) used a hypothetical example with maximal sprint speed to illustrate the utility of knowing in what contexts an organism approaches its maximal capacity in nature. In their example a hypothetical rodent species was said to differ in the percent of maximal capacity that it used in three contexts: escaping a predator, chasing prey, and chasing rival consexuals. Since it used 90% of maximal capacity while escaping predators but only 70% and 50% while chasing prey and rivals, respectively, they concluded that predator escape was likely the most important selective force on maximal sprint speed, since that was the only context during which it hypothetically used close to maximal capacity. This didactive example is not only instructive in demonstrating what "ecological performance" data can reveal, but the approach of looking at "ecological performance" in various potentially important contexts can be generally applied to other performance traits.

Quantifying the proportion of maximal capacity used may also reveal if individuals can compensate for a poor performance capacity. If no individuals in a population use close to their maximal capacity in a given context, then there may be some 'optimal' performance level below the maximal capacity of all individuals measured. Hence, if individuals do not utilize near-maximal performance in a given ecological

context, that context can be further ruled out as important to the evolution of that performance trait if there is a lack of compensation. However, if poor performers are found to behaviorally compensate in some ecological context (e.g., while escaping predators), it implies that there is selection on performance in that context and selective pressure for them to overcome their morphological and physiological deficits (Irschick 2000a, 2003). Individuals may compensate in numerous ways, but two broad categories are (1) a different behavioral strategy such as relying on crypsis instead of speed (Brodie 1992) and (2) increased percentage use of maximal capacity (Irschick 2003). For example, juvenile *Anolis lineatopis* lizards run slower than adults, but they utilize a higher percentage of maximal capacity than adults when escaping predators, presumably because predation is an important selective force on maximal sprint speed (Irschick 2000a).

The measurement of maximal performance and ecological performance at the individual level is critical to the study of compensation. Only at the individual level can one examine the potential for selection and the evolution of traits. If individual differences in ecological performance are detected, then an important issue is to understand what factors explain those differences. Hence, a question relevant to performance evolution is do slower individuals utilize a greater percentage of their maximal capacity than faster individuals? This leads to another question: is selection acting on maximal capacity of the performance trait, or is selection acting on the ability to compensate? In this paper I address these questions with a combination of laboratory and field studies on sprint speed in collared lizards (*Crotaphytus collaris*).

The collared lizard is a broadly distributed species in the southwestern United States that feeds opportunistically on available arthropods and small vertebrates (Blair and Blair 1941; Husak and McCoy 2000) using a sit- and-wait foraging style (Cooper et al. 2001). Males and females typically become sexually mature during their first year (hereafter "yearlings;" Baird et al. 1996; Baird and Timanus 1998), but males do not typically acquire and defend an exclusive territory until their second year (Baird et al. 1996). Among territorial males, sprint speed is positively correlated with territory size and number of females in the male's territory (Peterson and Husak in review; Husak 2005). Females do not defend territories in some Oklahoma populations (Baird et al. 1996), including the one I studied (Husak and Fox 2003a), but they do in other populations with different resource distributions (e.g., Baird and Sloan 2003). Therefore, the contexts in which maximal sprint speed might be important include predator escape, prey capture, and, for territorial males, chasing rivals out of a territory. I measured maximal sprint speed on a racetrack in the laboratory and compared it to field-utilized speeds of individual lizards while 1) escaping a predator, 2) chasing prey, and 3) responding to a rival consexual. By examining when collared lizards utilize near-maximal sprint speed in nature and when compensation is present, I sought to determine what selective forces operate on sprint speed in this species.

METHODS AND MATERIALS

General Methods

The study site was a 2-ha area on Sooner Lake dam in Pawnee County, Oklahoma, where the substrate consisted of concrete-covered rip-rap boulders. I captured adult (≥ 2 yr of age) and yearling (~ 1 yr of age) male and female lizards by

noosing. Each lizard was permanently marked by toe-clipping, and each was given a unique pattern of colored paint spots for visual identification at a distance (after Baird et al. 1996). Captured individuals that were marked the previous year as hatchlings were considered yearlings, whereas those marked the previous year before hatchlings emerged were considered ≥ 2 yr of age. I used surveying equipment to generate coordinates for scale maps of the study site and to determine home range sizes (see Husak and Fox 2003a, 2003b). The maps were scale representations of the study area with points designating numbered flags on the site. The flags were in close proximity (approximately 11 m apart) such that several could be seen from any given location, allowing accurate locations of each lizard by visual triangulation. I walked the site daily, observed lizards with binoculars, and mapped their locations. Territories were defined by the minimum convex polygon procedure (Rose 1982), using at least 20 sightings per lizard (Appendix 1).

Maximal Sprint Speed

At the peak of the breeding season (late May, Baird et al. 2001) of 2003 and 2004, I transported lizards to Oklahoma State University and held them for one day to encourage the passage of gut contents. No gravid females were used in these trials. On the mornings of the second and third days of captivity, I placed lizards individually in net bags inside a lighted incubator at 37°C. Three times a day (trials being separated by at least two hours), each lizard was removed from the incubator and immediately chased down a 3-m racetrack into a black bag at the end of the track. The racetrack was covered with a high-friction sandpaper substrate. I video taped runs on Hi8 film, following standard protocols (Braña 2003). I later viewed the tapes, counting the number of frames

it took for a lizard to traverse 1-m intervals. While this method may lose some resolution compared to measurements made with infrared beams, the purpose of my study was to compare maximal speeds to speeds obtained in the field. Since field speeds were also calculated using video tapes, this was a comparable method for obtaining maximal sprint speed. Also, speeds obtained using this method were similar to those found by Peterson and Husak (in review) using a racetrack with infrared beams. I classified the quality of each run as "good" or "poor" (van Berkum and Tsuji 1987), and data from "poor" runs (pauses, reversals) were discarded. Only the single fastest 1-m split for each run was analyzed. Immediately following a run, I measured the lizard's body temperature with a quick-read cloacal thermometer. I released all lizards at their exact point of capture after all trials were completed.

Field Sprint Speeds

To determine field performance I followed the methods of Irschick and Losos (1998). I measured sprint speeds for all sex and age classes at the height of the breeding season in three contexts: 1) escaping a predator, 2) foraging, and 3) while responding to an intruding rival consexual. No gravid females were used in these trials. The same generalized procedure of obtaining sprint speeds was used for all contexts. I used a videorecorder to record the movements of the lizards, then reviewed the tape in the field so that I could use landmarks to measure the distance ran for each movement. Hi8 film is recorded with 30 frames/sec, so I counted the number of frames per unit of distance measured in the field to obtain the sprint speed. If multiple movements occurred during a trial, I used the fastest speed. All trials were conducted when the substrate temperature

was 30-40° C, the optimal temperature range for collared lizards in central Oklahoma (Uzee 1990).

For the predator escape trials, a person (the same person in each case, wearing similar clothing) walked toward a lizard at a constant pace of approximately 40 m/min (e.g., Cooper 1997). I avoided making lizards run up or downhill the sloped dam since that may have affected behavioral anti-predator strategies (Jayne and Ellis 1998) and sprint performance (Irschick and Jayne 1999; Jayne and Irschick 2000). I attempted to control for this by walking toward the lizard parallel with the orientation of the dam.

To elicit foraging movements, I staged a foraging attempt by tethering a fishing fly (without the hook) to the end of a 4-m pole and placing it 3 m away from the lizard, slightly wiggling it at the spot on which it was placed (e.g., Irschick 2000b). I used this distance to match that used in the laboratory for maximal performance measurement. A wiggling fishing fly as a prey stimulus was appropriate because collared lizards are opportunistic foragers, relying primarily on motion to detect prey items while foraging (Sugarman and Hacker 1980). Lizard movements toward the fishing fly were video recorded, and speeds were calculated in the manner described above.

I staged intrusions of a non-neighboring male just inside the boundary of a resident male's territory, and 10 m away from the resident. Non-neighbors (captured > 2 km distant) were used to avoid any biases due to the "dear enemy" effect (Fox and Baird 1992). I introduced the unfamiliar intruders by tethering them, with approximately 8 cm of monofilament fishing line, to a 4.5-m pole and placing them at the desired location on a large rock (following Husak and Fox 2003b). Intruders were size-matched within 1 mm SVL of the size of the resident. Similar trials were conducted with female and

yearling intruders placed just inside the boundary of home ranges of females and yearlings, respectively. Once the intruder was in position, I recorded movement(s) by the occupant lizard toward the intruder and sprint speeds were calculated as described above. Henceforth, I refer to the intruders as "rivals," as they are potential competitors with the resident lizard for either mates, resources, or both.

Statistical Analysis

All data were $\log_{10}$-transformed for analysis, except proportion of sprint speed used in nature, which were arcsine-transformed. Data for each of the different sex and age classes from 2003 and 2004 did not significantly differ (t-tests; $p > 0.15$ for all), so the two years were pooled for analyses. Many of the same lizards were present in both years, but lizards used in one year were not used in the other. Sprinting, as measured in a laboratory environment, is determined by variation in motivation and responses to immediate environmental stimuli as well as underlying physiological and morphological differences (van Berkum and Tsuji 1987; Losos et al. 2002). I assessed repeatability of morphologically and physiologically constrained maximal capacity for sprint speed by calculating Pearson product-moment correlations (Hayes and Jenkins 1998) between the best and second-best performances of each individual, regardless of the day on which they occurred.

I made the comparisons among age and sex classes using ANOVA, followed by pairwise Tukey comparisons, for the following dependent variables: absolute maximal speeds, absolute field speeds, and proportion maximal capacity. Yearling males and females did not significantly differ in any variable measured ($t_{20} < 1.2$; $p > 0.26$ for all), except SVL (see Results below), so data for yearlings were combined for all further

analyses. To test for compensation within age classes I examined Pearson product-moment correlations between proportion of maximal capacity and maximal capacity. I used least-squares regression to determine if the slope of the line produced with field speed as the dependent variable and maximal capacity as the independent variable was significantly different from zero. When comparing among age and sex classes, a one-way ANOVA design was used with age/sex class as the factor. When comparing contexts within a sex or age class, a repeated measures design was used with context (foraging, escaping, responding to a consexual) as the factor. When there was no response from a lizard in a field trial, the individual was removed from that section of the analysis. Analyses were performed in SAS version 8 (SAS Institute 1999).

RESULTS

Differences Among Sex and Age Classes

A total of 22 yearlings (13 males, 9 females), 20 adult males, and 18 adult females had a complete set of data for analyses. There was a significant difference in SVL among territorial males, yearling males, yearling females, and adult females ($F_{3, 56} = 63.3$, $p < 0.001$), with all classes significantly differing from each other (Tukey's HSD, $p < 0.001$ for all) except adult females and yearling males (Tukey's HSD, $p = 0.97$). Adult males were the largest (mean SVL ± SEM = 103.8 ± 1.08), followed by adult females (mean SVL ± SEM = 92.0 ± 1.36), yearling males (mean SVL ± SEM = 91.5 ± 1.38), and yearling females (mean SVL ± SEM = 80.9 ± 0.79). All of the following analyses have male and female yearlings pooled. Maximal sprint speed capacity was highly repeatable ($r = 0.95$). There was a significant difference among all three age and sex classes in maximal sprint speed ($F_{2, 57} = 12.3$, $p < 0.001$; Fig. 1), with yearlings running

significantly slower than adult males ($p < 0.001$) and adult females ($p < 0.001$). There was no significant difference in maximal sprint speed between adult males and females ($p = 0.96$). There was also a significant difference among all three age and sex classes in sprint speed while foraging ($F_{2, 57} = 10.8$, $p < 0.001$; Fig. 1), escaping a predator ($F_{2, 57} = 5.2$, $p = 0.008$; Fig. 1), and responding to a rival ($F_{2, 25} = 358.4$, $p < 0.001$; Fig. 1). While foraging, yearlings ran significantly faster than adult males ($p = 0.05$) and adult females ($p < 0.001$), but adult males did not differ from adult females ($p = 0.07$). While escaping a predator, yearlings ran significantly faster than adult females ($p = 0.009$) but not adult males ($p = 0.87$), and adult males ran significantly faster than adult females ($p = 0.039$). While responding to a rival, adult males ran significantly faster than yearlings ($p < 0.001$) and adult females ($p < 0.001$). Yearlings did not differ from adult females ($p = 0.36$). In fact, only five of 18 adult females and three of 22 yearlings responded to a rival.

There was a significant difference among all three age and sex classes in proportion of maximal sprint speed used in the field while foraging ($F_{2, 57} = 178.2$, $p < 0.001$; Fig. 2), escaping a predator ($F_{2, 57} = 10.7$, $p < 0.001$; Fig. 2), and responding to a rival ($F_{2, 25} = 961.6$, $p < 0.001$; Fig. 2). While foraging, yearlings used a greater percentage of their maximal capacity than adult males ($p = 0.001$) and adult females ($p < 0.001$), but adult males and females did not differ ($p = 0.825$). Similarly, when escaping a predator, yearlings used a greater proportion of maximal capacity than adult males ($p = 0.028$) and adult females ($p < 0.001$), but adult males and females did not differ ($p = 0.126$). While responding to a rival, adult males used a significantly higher proportion of their maximal capacity than both yearlings ($p < 0.001$) and adult females ($p < 0.001$). Yearlings did not differ from adult females ($p > 0.99$).

Differences Within Sex and Age Classes

Within adult males, there was a significant difference in sprint speed among contexts ($F_{3, 70.2} = 220.6$, $p < 0.0001$; Fig. 1), where maximal sprint speed was not significantly different from the speed used while responding to a rival ($p = 0.086$), but all other contexts were significantly different from each other ($p < 0.0001$ for all; Fig. 1). Within adult females, there was a significant difference among contexts ($F_{3, 68} = 748.7$, $p < 0.0001$; Fig. 1), and all contexts were significantly different from each other ($p < 0.0001$ for all; Fig. 1). Within yearlings there was a significant difference among contexts ($F_{3, 68} = 678.3$, $p < 0.0001$; Fig. 1). As in adult females, all contexts were significantly different from each other ($p < 0.0001$ for all; Fig. 1).

There was a significant difference in the proportion of maximal sprint speed capacity used in nature among contexts for adult males ($F_{2, 53.8} = 126.5$, $p < 0.0001$; Fig. 2), adult females ($F_{2, 51} = 159.8$, $p < 0.0001$; Figure 2), and yearlings ($F_{2, 59.6} = 269.1$, $p < 0.0001$; Fig. 2). All contexts were significantly different from each other in each age and sex class ($p < 0.0001$ for all; Fig. 2).

Compensation Within Sex and Age Classes

In adult males there was a significant negative correlation between maximal sprint speed and the proportion used while foraging ($r = -0.70$, $p = 0.001$; Figure 3A) and while escaping a predator ($r = -0.82$, $p < 0.001$; Fig. 3A). Similar relationships were found for adult females (foraging: $r = -0.48$, $p = 0.046$; escaping a predator: $r = -0.65$, $p = 0.003$; Fig. 3B) and yearlings (foraging: $r = -0.83$, $p < 0.001$; escaping a predator: $r = -0.84$, $p < 0.001$; Fig. 3C). Because so few yearlings and adult females responded to rivals (see above), I did not attempt to correlate maximal capacity with proportion used in this

context. In adult males, there was no correlation between maximal capacity and proportion used while responding to a rival ($r = -0.17$; $p = 0.48$; Fig. 3A).

In adult males the slope of the line produced from regressing foraging sprint speed on maximal sprint speed was not significantly different from zero ($r = -0.35$, $t = -1.59$, $p = 0.13$; Fig. 4A), but it was marginally different from zero while escaping a predator ($r = -0.44$, $t = -2.10$, $p = 0.05$; Fig. 4A). No slopes were different from zero for adult females (foraging: $r = -0.09$, $t = -0.35$, $p = 0.73$; escaping a predator: $r = -0.31$, $t = -1.32$, $p = 0.20$; Fig. 4B). For yearlings, the slope of the line produced from regressing foraging sprint speed on maximal sprint speed was negative and significantly different from zero ($r = -0.76$, $t = -5.21$, $p < 0.001$; Fig. 4C), but not when escaping a predator ($r = 0.29$, $t = 1.36$, $p = 0.19$; Fig. 4C). Because so few yearlings and adult females responded to rivals (see above), I did not attempt to examine this context for these demographic groups. In adult males, the slope of the line was positive and significantly different from zero while responding to a rival ($r = 0.85$; $t = 6.704$, $p = < 0.001$; Fig. 4A).

DISCUSSION

Maximal locomotor capacity in collared lizards is under the influence of several selective pressures that vary in intensity depending on age and sex. Yearlings and adult females utilized speeds near-maximal capacity while escaping predators, but much less so while foraging or when responding to rival consexuals. Adult males, however, used speeds closer to maximal capacity while responding to rival adult males in their territory, followed by escaping a predator, and then foraging. This implies that predator avoidance is likely the strongest selective agent on maximal locomotor capacity for yearlings and adult females, whereas the strongest selective pressure on adult males is likely sexual

selection for territory maintenance. Braña (2003) obtained similar results with wall lizards (*Podarcis muralis*), where males attained high speeds during intraspecific pursuits and when escaping predators. Wall lizards and collared lizards are distantly related, implying that sexual selection as a force operating on maximal sprint speed may be more widespread than was previously considered.

Examination of how individuals compensate in the three ecological contexts also shed light on their relative importance as selective pressures on sprint speed. Broadly, yearlings appear to be compensating for their poor maximal capacity compared to that of adults. Yearlings have a significantly lower absolute maximal capacity, and to compensate they utilize speeds closer to maximal capacity than adults. This agrees with previous work on *Anolis lineatopus* (Irschick 2000a). This implicates strong pressure to attain some sufficient speed to efficiently escape predators (see below), and yearlings must use speeds close to their maximal capacity.

Yearlings, adult females, and adult males were all found to compensate while escaping predators and foraging. That is, individuals with lower maximal capacity used a greater proportion of their maximal capacity in these contexts than those individuals that had a greater maximal capacity. Not one was found to compensate while responding to a rival consexual within their territory or home range. However, the reason for the lack of compensation in this context differed between the ages and sexes. Very few yearlings or adult females responded to rivals, and, of those, none utilized near maximal capacity. This makes sense, because neither group is territorial (Baird et al. 1996; Husak and Fox 2003a). However, under the right circumstances, yearling males may obtain territories (Baird and Timanus 1998), and I predict that the response to rivals would escalate and the

proportion of maximal capacity used when responding to rivals would increase. Adult males showed no compensation in this context because all adult males used near-maximal capacity when responding to rival males in their territory. That is, no matter how fast they were, they still used near-maximal capacity while responding to an intruding rival. Further, individuals having the capacity to run faster did run faster in this context than individuals with lower maximal capacity (Fig. 4C). These observations strengthen the above argument that sexual selection exerts strong pressure on maximal sprint speed capacity in adult male collared lizards, and it explains concurrent work showing a positive relationship between maximal sprint speed and estimates of mating success in this population (Husak 2005). Lizards with faster maximal capacity have the ability to more effectively cover a larger area and defend their territory from rivals than slower individuals. Those with a low maximal capacity that attempt to defend an area that is too large will likely have mates usurped by neighboring rivals, resulting in a decrease in their relative fitness.

The proportion of maximal capacity used in nature in various ecological contexts, taken together with the degree of locomotor compensation in those contexts, can reveal patterns that may not be apparent if only a performance-fitness correlation were examined. It is critical to understand how organisms utilize whole-animal performance before we can understand what the relative importance of different selective pressures is. Further, looking only at field-use of maximal capacity, and not also at individual compensation, may lead to an unclear picture of how maximal capacity may be important to the organism. For collared lizards, there are obvious sex and age differences in which selective forces are important to the evolution of maximal sprint speed. By looking at the

proportion of maximal capacity used, it appears that territorial defense is most important for adult males, followed by predator escape. For yearlings and adult females, predator escape appears to be the most important. The relative importance of foraging remains ambiguous from these data.

Previous work has suggested that predator escape and foraging are the most important selective pressures operating on maximal sprint speed in lizards, especially those that are sit-and-wait foragers (see references above). If this is a true generalization, why did I find somewhat low values of percent of maximal capacity used in these contexts? One possibility is that the methodology employed, simulated predator and prey encounters, underestimated what lizards would utilize in natural encounters. The lack of a positive relationship between escape-behavior field speeds and maximal capacity supports this possibility to some extent. A greater predatory threat might have required a greater 'optimal' speed of escape, producing a positive (or asymptotic) relationship between field speeds and maximal speeds. The primary predators of collared lizards are snakes (Husak et al. in review). Snakes are very likely much less visible to the lizards in nature and may be able to approach closer than a large, conspicuous human "predator." If real predators can approach closer, then maximal sprint speed may be necessary for escape. Further, it was often not necessary for lizards to run far to find refuge. One advantage of having a territory or home range is acquiring familiarity with the immediate environment, especially the location of refugia (Baird and Liley 1989; Baird and Sloan 2003). Nevertheless, there are likely times when an individual is threatened by a predator after having moved away from known refugia while foraging or interacting with conspecifics. Under such conditions it would need to use a greater proportion of its

maximal capacity to escape. My finding of compensation adds to the likelihood that predator escape is important to the evolution of maximal capacity.

What, then, about foraging? Methodology is likely not a problem, as lizards readily responded to the stimulus and tried to eat it. There was compensation, suggesting that there may be some selective pressure to be fast while foraging. However, the speed that must be attained is likely much lower than the average maximal capacity, suggesting that foraging proficiency may not be very important to the evolution of maximal sprint speed. A similar proposition was made for marine iguanas (Wikelski and Romero 2003). My conclusions are further supported by the lack of a positive relationship between field speeds used while foraging and maximal capacity (Fig. 4). The finding that yearlings use a greater proportion of maximal capacity while foraging relative to adults may be the result of foraging inexperience. However, the significant negative relationship between field speeds while foraging and maximal capacity is intriguing. Why would slower individuals run faster in nature while foraging than faster individuals? Similarly, why do slower adult females run faster than maximally faster individuals while escaping predators? It would be instructive to know how the proportion of maximal capacity used and the absolute field speeds used changes during ontogeny and what costs are associated with using near-maximal capacity.

In summary, collared lizards utilize near-maximal sprint speed capacity in some, but not all, ecological contexts. Further, the relative importance of different selective pressures differs between the sexes and during ontogeny. Although natural seletion for predator avoidance is likely a strong selective force acting on locomotor performance in collared lizards, especially in yearlings and adult females, intra-sexual selection for

territory maintenance may be a stronger selective agent on males. I found that in adult females and yearlings, slower individuals ran faster in some contexts in nature than did individuals with greater capacity for speed. These are puzzling results and emphasize our lack of knowledge of how animals use maximal capacity in nature and what costs are associated with using near-maximal capacity. These results stress the importance of studying field-use of performance in nature and comparing it to maximal capacity in the same individuals. This will allow further resolution of links between morphology, performance, behavior, and fitness.

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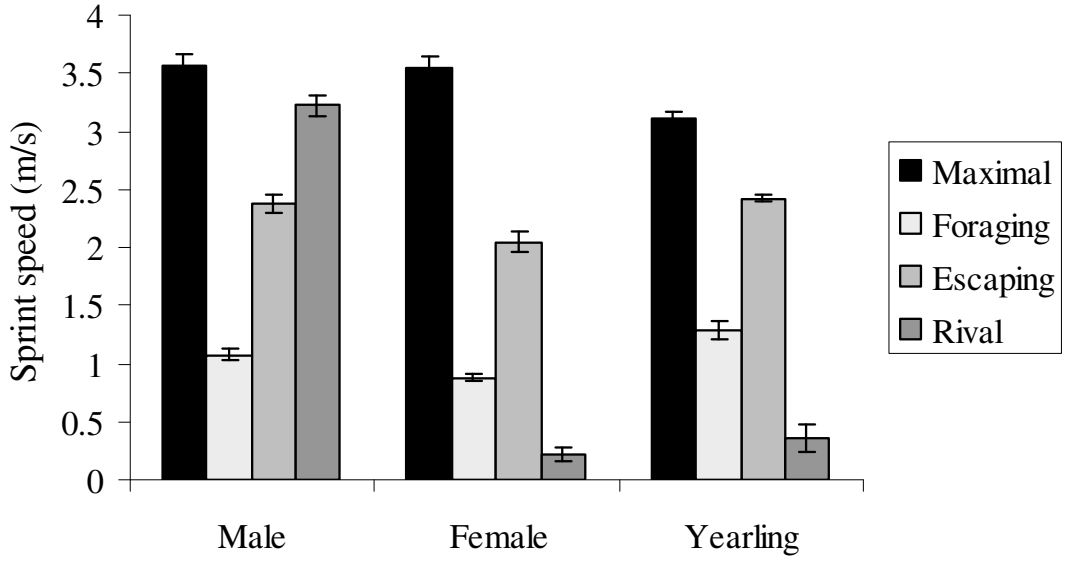
Figure Legends:

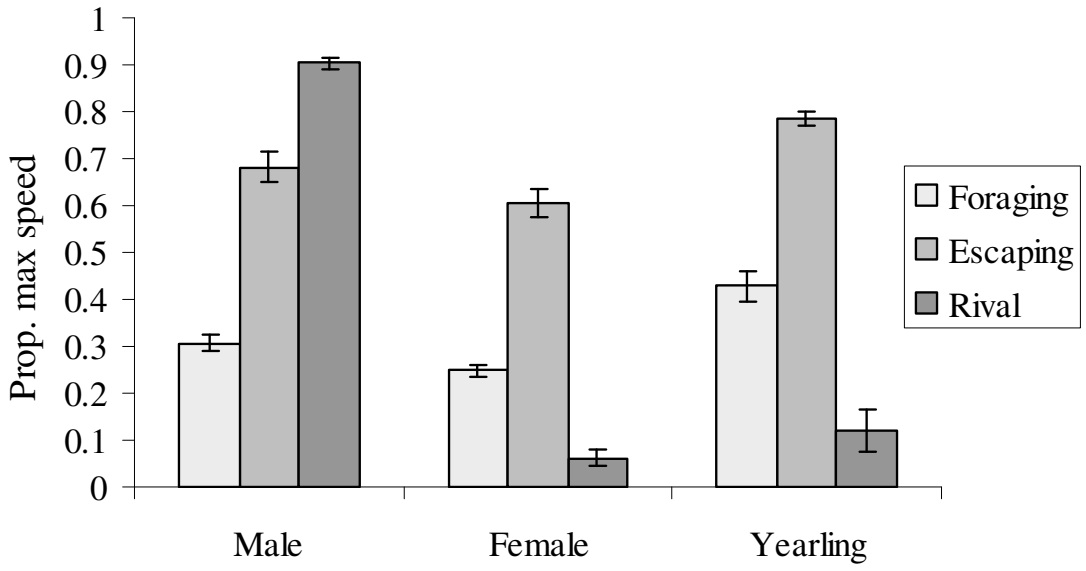
Fig. 1. Sprint speeds attained by collared lizards in the laboratory (maximal), and in three ecological contexts in nature. See text for details. Bars represent means ± 1 SEM.

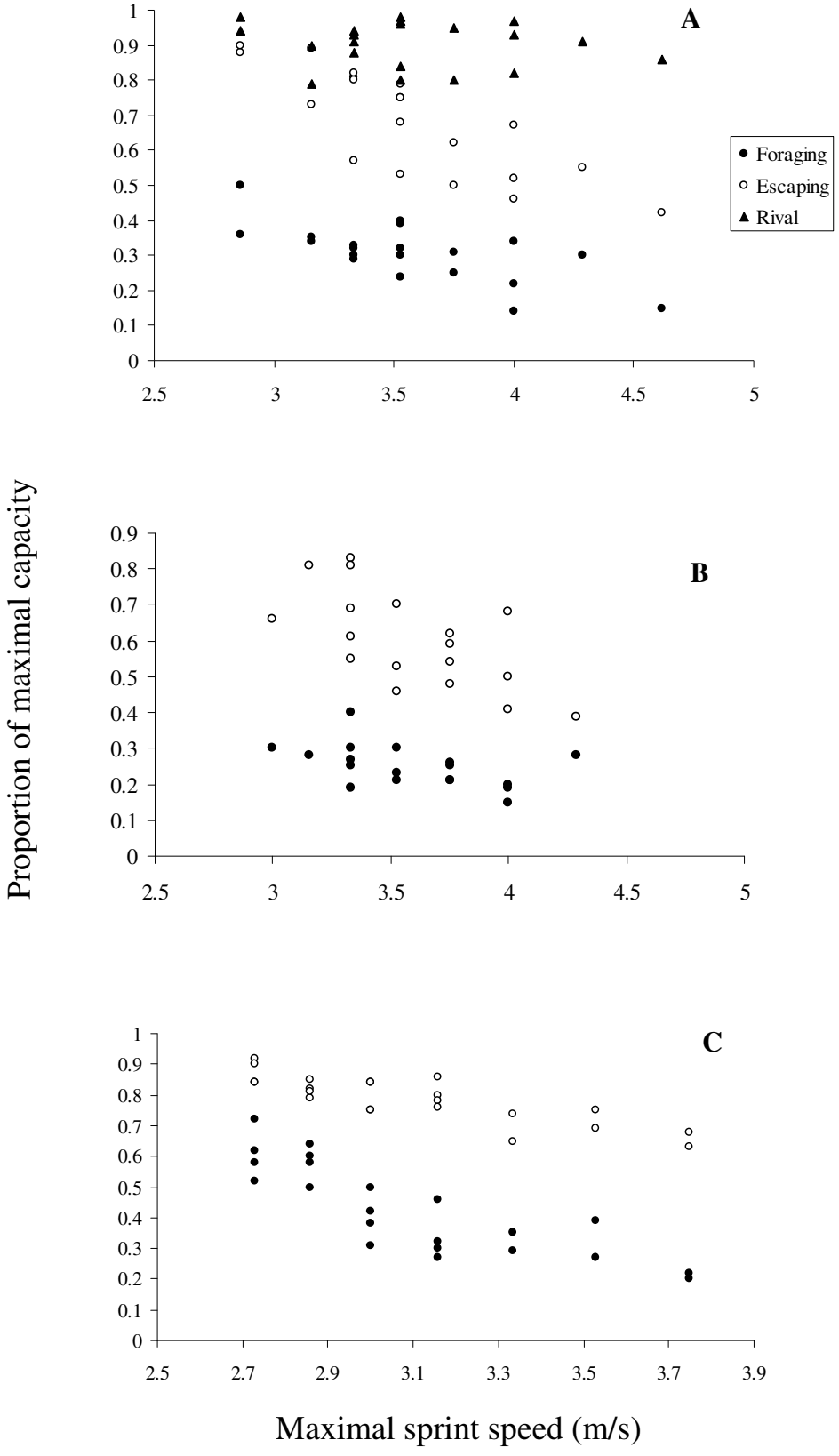
Fig. 2. Proportion of maximal sprint speed capacity used by collared lizards in three ecological contexts in nature. See text for details. Bars represent means ± 1 SEM.

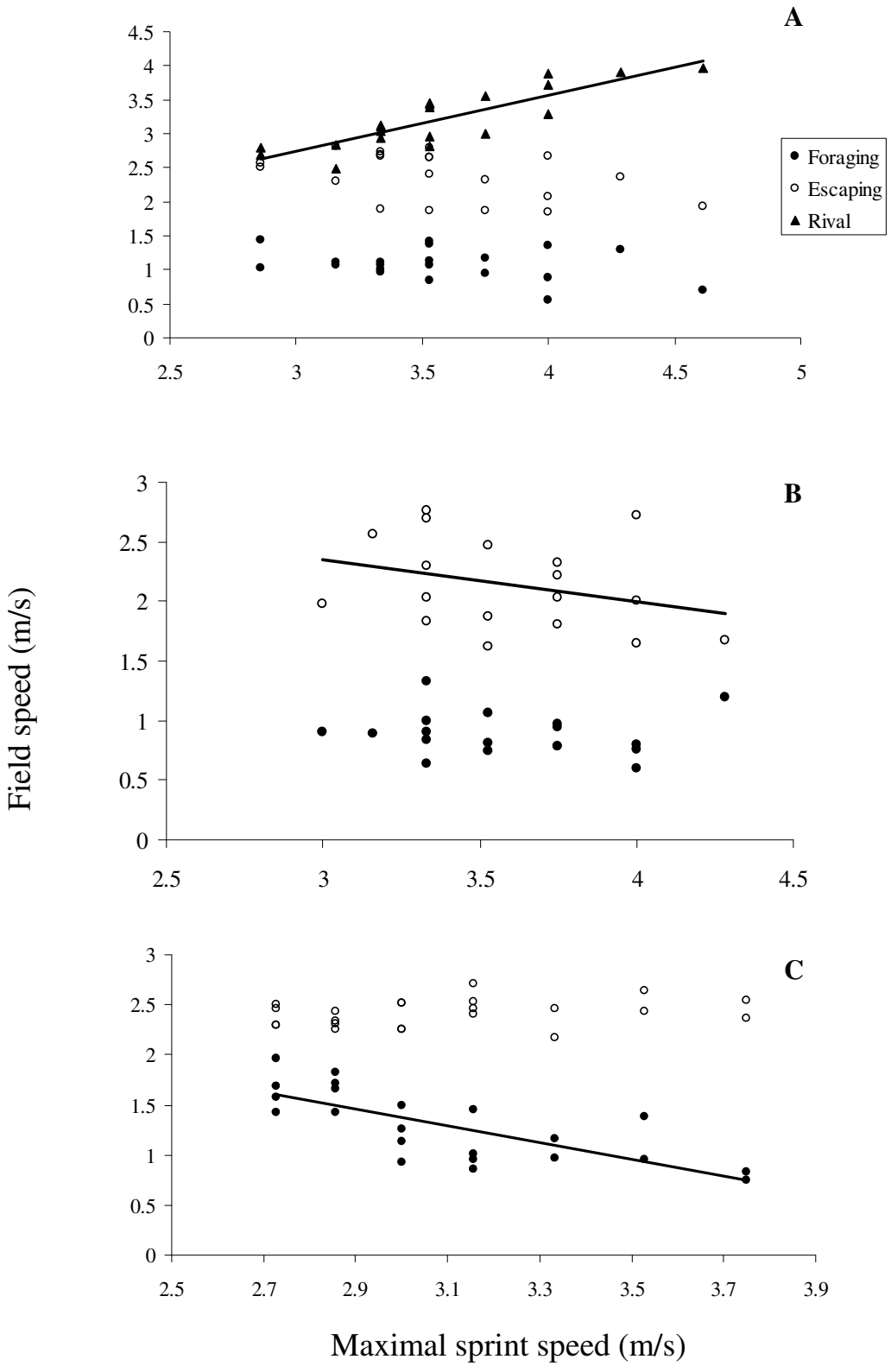
Fig. 3. Proportion of maximal sprint speed capacity used by collared lizards in three ecological contexts in nature plotted against maximal sprint speed capacity as determined in the laboratory for (A) adult males, (B) adult females, and (C) yearlings.

Fig. 4. Absolute sprint speeds used by collared lizards in three ecological contexts in nature plotted against maximal sprint speed capacity as determined in the laboratory for (A) adult males, (B) adult females, and (C) yearlings.


Sprint speed (m/s)
4
3.5
3
2.5
2
1.5
1
0.5
0
Male
Female
Yearling
Maximal
Foraging
Escaping
Rival


Prop. max speed
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Male
Female
Yearling
Foraging
Escaping
Rival


A
B
C
Foraging
Escaping
Rival
Proportion of maximal capacity
Maximal sprint speed (m/s)


A
B
C
Foraging
Escaping
Rival
Field speed (m/s)
Maximal sprint speed (m/s)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
2.5
3
3.5
4
4.5
5
2.7
2.9
3.1
3.3
3.7
3.9

DO FEMALE COLLARED LIZARDS CHANGE FIELD USE OF MAXIMAL SPRINT SPEED CAPACITY WHEN GRAVID?

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Summary

1. Locomotor ability is well documented to decrease in gravid female lizards. However, no studies have examined what proportion of maximal sprint speed capacity gravid females use in nature or how a reduction in maximal capacity translates to a change in sprint speeds used in nature. Gravid females may compensate for reduced locomotor ability by increasing the proportion of their maximal capacity used in nature, or by changing their antipredator behaviour.

2. Maximal sprint speed was measured in the laboratory for female collared lizards (*Crotaphytus collaris*) while gravid and non-gravid and compared to field-used speeds while foraging and escaping predators, also while gravid and non-gravid.

3. Females had significantly lower maximal sprint speed capacity while gravid, and they ran slower while foraging and escaping predators. However, gravid females did not increase the proportion of maximal capacity used in those contexts compared to when not gravid.

4. Gravid females compensated for reduced locomotor capacity by staying closer to refugia and not by remaining more cryptic.

5. These results suggest that the costs of reduced locomotor capacity may not be associated with direct costs while foraging or escaping predators, but instead with the indirect effects associated with the change in antipredator behaviour.

Introduction

Life-history traits reflect trade-offs among various components of fitness, such as fecundity and survivorship (Stearns 1976, Roff 1992). It is predicted that reproduction should entail costs that result from the tradeoff between current and future reproductive investment (Reznick 1985, Stearns 1989, 1992), and these costs generally take the form of survival or fecundity costs (Bell 1980, Shine 1980, Brodie 1989, Miles, Sinervo & Frankino 2000). Survival costs can be further divided into those involving metabolic tradeoffs and those involving 'ecological' costs such as increased risk of predation or reduced whole-animal performance (Miles et al. 2000). Among survival costs, reduced locomotor performance in pregnant or gravid females is perhaps the most well known and studied (e.g., Bauwens & Thoen 1981, Shaffer & Formanowicz 1996, Sinervo & DeNardo 1996, Cuthill & Houston 1997 and references therein). A large majority of these studies compared maximal sprint speeds of gravid versus non-gravid females (Shine 2003) and found reduced locomotor capacity as the result of a 'physical' burden associated with increased mass (Shine 1980) and/or a 'physiological' burden associated with altered metabolic pathways and hormone profiles (Olsson, Shine, and Bak-Olsson 2000). It is generally understood that gravidity reduces maximal locomotor capacity as measured in a laboratory, but it is unclear how reduced locomotor capacity translates to costs in nature. Indeed, while it is typically presumed that maximal locomotor abilities place constraints on such tasks as foraging and escaping predators (Bennett & Huey

1990), there is little supporting evidence for this proposition (Garland & Losos 1994, Irschick & Garland 2001).

Gravid females with reduced locomotor capacity may compensate in various ways. They may use a greater proportion of their maximal capacity to continue running fast (Irschick 2003, Husak 2005). They may rely more heavily on crypsis than on speed, as seen in several lizard species (e.g., Bauwens & Thoen 1981, Brodie 1989, Cooper et al. 1990). They may also increase defensive behaviour, as in scorpions (Shaffer & Formanowicz 1996). It is difficult to predict how females will compensate for reduced maximal locomotor performance without knowing the relevance of maximal sprint speed in natural situations. This uncertainty can be attributed largely to our general lack of knowledge regarding whether animals use maximal capacity in nature (Irschick 2003). If females do not use maximal capacity in nature, then a reduction in that trait, as measured in the laboratory, may not be relevant and may not impose a cost of reproduction. For example, some female *Anolis* lizards do not utilize near-maximal capacity while foraging, but they do when escaping predators (Irschick 2000, Irschick & Losos 1998), and this difference is also seen in non-gravid collared lizards (*Crotaphytus collaris*; Husak 2005). These results imply little if any foraging cost associated with reduced maximal capacity, especially for sit-and-wait foraging species such as anoles and collared lizards. However, there is the potential for a predation cost, and females may compensate by changing their escape behaviour or using a greater proportion of their maximal capacity to attain a sufficient escape speed.

I sought to examine compensatory behaviour in gravid collared lizards by measuring maximal sprint speed capacity in the laboratory and field-use of maximal

capacity. First, I wanted to determine whether or not female collared lizards have reduced locomotor performance when gravid. Second, I wanted to determine if non-gravid females use maximal capacity in nature, and whether or not this changes when they are gravid. If females use near-maximal capacity when not gravid, do they compensate while gravid by using speeds that are closer to their maximal capacity? Third, do females change their anti-predator behaviour when gravid as an alternative, or additional, means of compensating for reduced locomotor capacity?

Materials and methods

The study site was a 2-ha area on Sooner Lake dam in Pawnee County, Oklahoma, where the substrate consisted of concrete-covered rip-rap boulders. Lizards were captured by noosing and permanently marked with toe-clips and a unique pattern of colored paint spots for visual identification at a distance (after Baird, Acree & Sloan 1996). At two times during the 2003 breeding season lizards (the same individuals, once while gravid, once when not gravid) were transported to Oklahoma State University and held individually in net bags for one day to encourage the passage of gut contents. Gravidity is easily assessed in collared lizards by palpating their abdomen (Baird 2004). For this study gravid females had eggs greater than approximately 8 mm maximum diameter with the eggs in the late, round vitellogenic stage or the early, oval shelling stage.

On the mornings of their second and third days of captivity, lizards were placed inside a lighted incubator set at 37°C. Three times a day at intervals of at least two hours, each lizard was removed from the incubator and immediately chased down a 3-m racetrack into a black bag at the end of the track. The racetrack had a high-friction

sandpaper substrate. Instead of using a racetrack with vertically paired infrared photocells, runs were video taped on Hi8 film (after Braña 2003). The tapes were later viewed and the number of frames it took for a lizard to traverse 1-m intervals was counted. Speeds obtained in this method were comparable to those found for this species by Peterson and Husak (in review) using a racetrack with infrared beams. The quality of each run was classified as "good" or "poor" (van Berkum and Tsuji 1987), and data from "poor" runs (pauses, reversals) were discarded. The single fastest 1-m split for each run was analyzed. The best and second-best performances of each individual, regardless of the day on which they occurred, indicated high repeatability for gravid ($r = 0.94$, $p < 0.001$) and non-gravid females ($r = 0.92$, $p < 0.001$). All lizards were released at their exact point of capture after all trials were completed.

The methods of Irschick & Losos (1998) and Husak (2005) were used to determine speeds used in nature. Sprint speeds were measured at the height of the breeding season on the same individuals while gravid and while non-gravid in two contexts: 1) foraging and 2) escaping a predator. The same generalized procedure of obtaining sprint speeds was used for both contexts. A video camera was used to record movements of the lizards, and the tape was reviewed in the field so that landmarks could be used to measure the distance ran for each movement. Hi8 film is recorded with 30 frames/sec, so I counted number of frames per unit of distance measured in the field to obtain sprint speed. If multiple movements occured during a trial, the fastest speed was used for analyses. All trials were conducted when substrate temperature was 30-40° C, the optimal temperature range for collared lizards in central Oklahoma (Uzee 1990). For the predator escape trials, a person (the same person in each case, wearing similar

clothing) walked toward a lizard at a constant pace of approximately 40 m/min and from a constant direction, recording where the observer was in relation to the lizard when it ran (approach distance, Cooper 1997) and to where the lizard ran (flight distance, Cooper 1997). For the foraging movements, a foraging attempt was staged by tethering a hookless fishing "fly" to the end of a 4-m pole and placing it 3 m away from the lizard and slightly wiggling it (e.g., Husak 2005). Movements toward the fishing fly were video recorded, and speeds were calculated in the manner described above.

I calculated proportion of maximal sprint speed capacity used in each context separately for gravid and non-gravid females. All data were $\log_{10}$-transformed for analysis, except proportion of maximal sprint speed used in nature, which was arcsine-transformed. Paired t-tests were used to look for differences between gravid and non-gravid females in mass, maximal sprint speed, absolute speed used while foraging, absolute speed used while escaping a predator, proportion of maximal sprint speed used in foraging, proportion of maximal sprint speed used in escaping a predator, approach distance, and flight distance.

Results

All data were obtained for 15 females. As expected, gravid females were significantly heavier than non-gravid females ($t_{14} = 10.05$, $p < 0.001$). Non-gravid females had significantly faster maximal sprint speed than gravid females ($t_{14} = 21.01$, $p < 0.001$; Figure 1). Similarly, non-gravid females ran significantly faster than gravid females while foraging ($t_{14} = 5.086$, $p < 0.001$; Figure 1) and escaping predators ($t_{14} = 9.1$, $p < 0.001$; Figure 1). There was no significant difference between gravid and non-gravid females in proportion of maximal sprint speed capacity used while foraging ($t_{14} =$

0.20, p = 0.841; Figure 2) or escaping a predator ($t_{14} = 2.04$, p = 0.060; Figure 2). Gravid and non-gravid females also did not significantly differ in approach distance ($t_{14} = 1.32$, p = 0.21; Figure 3). However, flight distance was significantly shorter in gravid females than in non-gravid females ($t_{14} = 2.50$, p = 0.025; Figure 3)

Discussion

Gravidity reduced the maximal sprint speed capacity of female collared lizards as measured in the laboratory, as well as the speed at which they ran in nature while foraging and escaping predators. Non-gravid and gravid females did not use maximal capacity while foraging or escaping predators, but speeds used when escaping predators were closer to maximal capacity than those used when foraging. However, females did not compensate for reduced maximal capacity while gravid by increasing the proportion of maximal capacity used in nature. Instead, females altered their escape behaviour.

Contrary to some previous studies (Bauwens & Thoen 1981, Brodie 1989, Cooper et al. 1990), gravid females did not rely more on crypsis and decrease the distance between themselves and an approaching predator before fleeing. Instead, they decreased the distance they ran when a predator approached. This suggests that either gravid females are closer to refugia than non-gravid females are, or that non-gravid females are more likely to risk running a longer distance when a predator approaches. The first hypothesis predicts that gravid females would not need to attain a high speed to escape, because they can enter a refuge close to where they are perched. Such females may be using their home range efficiently and to their advantage in escaping potential predators. Baird & Sloan (2003) argued for this hypothesis in a population of collared lizards in central Oklahoma where females defended core areas surrounding a perch rock with a

refuge underneath it. The second hypothesis implies that non-gravid females lack one or another cost associated with being gravid, for example reduced locomotor capacity, physiological costs associated with egg production, or reduced body temperatures due to gravidity.

It is well known that gravid female lizards typically have lower body temperatures than non-gravid individuals (Beuchat 1986, Mathies & Andrews 1997, Le Galliard, Le Bris & Clobert 2003 and references therein, but see Labra & Bozinovic 2002). Similar to how lower body temperatures in gravid females can result in a behavioral shift when responding to a predator (Cooper 2000), the reduction in field speeds of gravid females may reflect generally lower body temperatures as a result of gravidity. Sprint speed in many species is temperature-dependent (Huey & Kingsolver 1989), but without data on body temperatures of field-active lizards during the activities measured in this study it is difficult to comment on this hypothesis. Lower body temperatures may lead to decreased foraging proficiency and/or predator escape by reducing sprint speed in the field. This indirect effect may not be detected if only maximal capacity is examined, even in conjunction with escape behaviour data. An alternative hypothesis for the observed change in antipredator behaviour could be the opposite direction of causation where reduced locomotor capacity of gravid female collared lizards resulted in a change in escape behaviour, thereby lowering body temperatures (Braña 1993) by preventing them from either basking in optimal locations or spending an optimal amount of time basking.

Many other species of lizards compensate for reduced locomotor capacity by changing their escape behaviour to rely more on crypsis (Bauwens & Thoen 1981, Brodie 1989, Cooper et al. 1990). Why did female collared lizards not compensate in a similar

manner? Unlike otherlizards that have been found to rely more on crypsis while gravid, female collared lizards are visually more conspicuous in their environment when gravid due to the presence of large orange spots and bars on the dorsolateral portion of the trunk (Ferguson 1976, Macedonia, Brandt & Clark 2002, Baird 2004). Even if the visual systems of collared lizard predators are different than that of human observers, which they most likely are, the intensity contrast alone would make gravid female collared lizards conspicuous against the gray rocks of Sooner Lake (Macedonia et al. 2004). Future work may find a general pattern across lizards species, where species with females that exhibit "bright" gravid coloration (reviewed in Cooper & Greenberg 1992) compensate by perching closer to refugia instead of relying on crypsis.

The results of this study have interesting implications for how reduced locomotor capacity might be costly to gravid females. Sloan & Baird (1999) found that female collared lizards increased activity after oviposition and suggested that performance of gravid females may be compromised by the burden of eggs. However, for female collared lizards the cost of gravidity is likely not a foraging cost in the sense that gravid females cannot attain speeds to capture prey; nor is it likely a direct predation cost where females cannot attain speeds to escape predators. Although females ran significantly slower while gravid in these contexts, the fact that they did not increase the proportion of maximal capacity used suggests that slower speeds were not costly. However, "close calls" where predators manage to get very close to a female may represent a situation in which fast sprint speeds are important. In such cases, gravid female perhaps cannot attain a speed fast enough to reach a refuge even if it is close. Further, if gravid females are remaining closer to refugia, they may have a limited foraging radius. Thus, costs are

likely to manifest themselves when gravid females move further from known refugia in order to forage, or when they re-emerge after seeking refuge from a predator, and when, with lower body temperatures, they have even more reduced sprint speed capacity.

Understanding how animals utilize maximal capacity in different ecological contexts and how those patterns change during the reproductive cycle can reveal surprising patterns. Gravid female collared lizards do not compensate for reduced locomotor ability by increasing the proportion of maximal capacity used while gravid, but instead they change their escape behavior. These results accentuate the fact that much remains to be studied before the direct and indirect ecological costs of gravidity are completely understood. Future studies that simultaneously address the interplay of gravidity, body temperature, field use of sprint speed, and antipredator behaviour would be enlightening to our understanding of reproductive costs.

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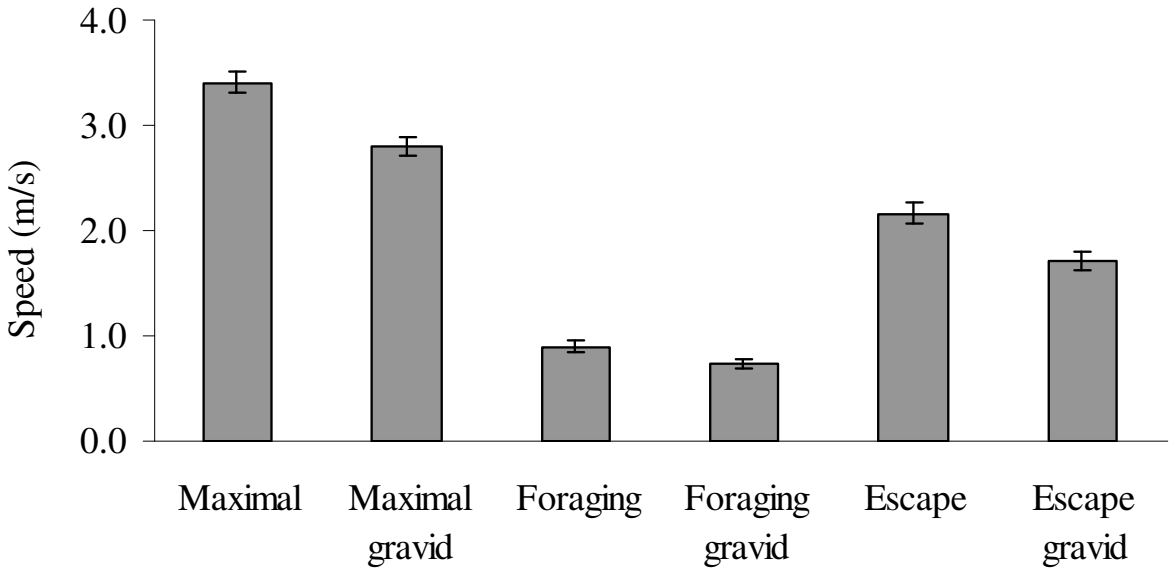
Figure Legends:

Fig. 1. Sprint speeds attained by gravid and non-gravid female collared lizards in the laboratory (maximal), and in two ecological contexts in nature. See text for details. Bars represent means ±1 SEM. Asterisks represent a significant difference at $p < 0.001$.

Fig. 2. Proportion of maximal sprint speed capacity used by gravid and non-gravid female collared lizards in two ecological contexts in nature. See text for details. Bars represent means ±1 SEM.

Fig. 3. Antipredator behaviour of gravid and non-gravid female collared lizards. Approach distance is the distance between the predator and the lizard when the lizard fled. Flight distance is the distance ran after the lizard fled from the predator. Bars represent means ±1 SEM. The asterisk represent a significant difference at $p < 0.05$.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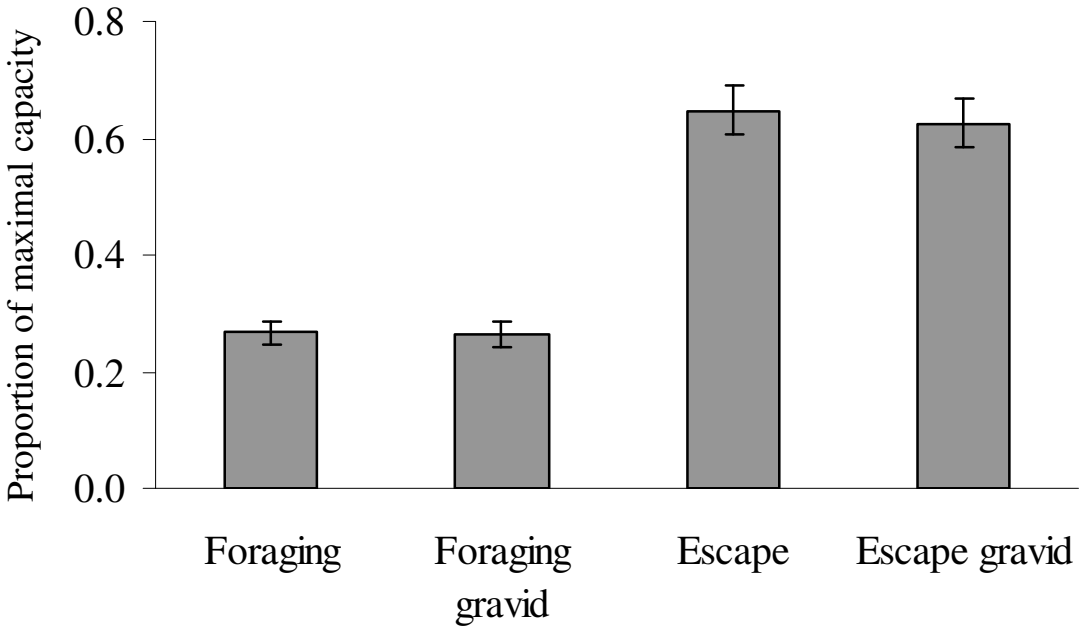
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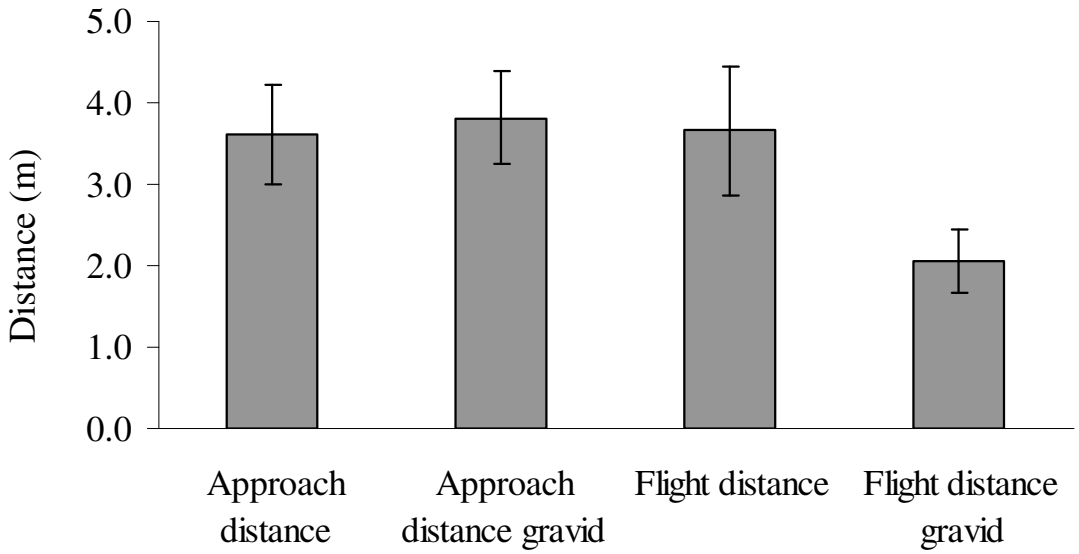
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DOES SPEED HELP YOU SURVIVE?
A TEST WITH COLLARED LIZARDS OF DIFFERENT AGES

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Summary

1. While it is generally accepted that the evolution of morphological traits is mediated by selection on whole-animal performance, few studies have examined how variation in performance explains variation in fitness. Most studies to date have studied how performance predicts survival, and these typically examine only a single age class.

2. Maximal sprint speed was measured for hatchling and adult collared lizards (*Crotaphytus collaris*), in addition to morphological measurements, in order to determine how well annual survival could be predicted by performance and whether the relationship between performance and survival differed between age classes.

3. Logistic regression revealed that no morphological trait or sprint speed performance predicted survival in adults. However, sprint speed predicted survival in hatchlings. Further, hindlimb length differed between survivors and non-survivors and correlated with sprint speed, suggesting that the evolution of hindlimb length in hatchlings may be driven by selection on sprint speed performance.

4. Selection on sprint speed may be mediated directly by predators where hatchlings cannot attain speeds sufficient to escape predators or indirectly where slower individuals

use a greater proportion of their maximal capacity than faster individuals while escaping predators, perhaps causing elevated stress levels or a higher expenditure of energy stores.

Introduction

Differential survival among individuals reflects variation in underlying morphological and physiological traits, but selection acts on the integrated manifestation of such traits (i.e., whole-animal performance; Huey & Stevenson 1979, Arnold 1983). Since Arnold (1983) described an operational framework for linking morphology, performance, and fitness, many authors have extended and refined his paradigm (e.g., Bennett & Huey 1990, Wainwright & Reilly 1994, Irschick 2002). The link between morphology and performance has received considerable attention (reviewed in Garland & Losos 1994, Irschick & Garland 2001), whereas the link between performance and fitness has received comparatively little (Irschick & Garland 2001). The lack of studies is likely due to the difficulty of quantifying both physiological performance and life-time fitness in the same individuals. Studies attempting to do so have focused on how performance predicts survival (e.g., Jayne & Bennett 1990, Miles 2004) typically within a specific age class. These studies have been instructive regarding how natural selection may act on performance, and they have revealed dramatic ontogenetic differences in how selection acts on performance (Jayne & Bennett 1990, Kingsolver 1999, Warner & Andrews 2002, Kingsolver & Srygley 2002, Miles 2004). Locomotor performance predicted survival in hatchling lizards, *Sceloporus undulatus* (Warner & Andrews 2002) and *Urosaurus ornatus* (Miles 2004), but not hatchlings of garter snakes, *Thamnophis sirtalis* (Jayne & Bennett 1990) or *S. occidentalis* and *S. merriami* hatchlings (unpublished studies cited in Huey & Bennett 1990). Juvenile endurance capacity predicted survival in the lizard

Lacerta vivipara (Le Galliard, Clobert, & Ferrière 2004). Among adults, locomotor performance predicted survival in garter snakes (Jayne & Bennett 1990), but flight performance did not predict survival in three butterfly species (Kingsolver 1999, Kingsolver & Srygley 2002). More studies examining how performance predicts survival in different age classes of the same species are needed to assess the generality of ontogenetic shifts in selection on performance.

Ontogenetic differences in selection on performance would not be surprising given that absolute performance typically differs between juveniles and adults. Performance typically scales with body size such that younger individuals are "worse" absolute performers than adults due to their smaller size (Garland & Losos 1994, Carrier 1996, Irschick 2000). Although there are many instances of juveniles using very different niches than adults, juveniles in many vertebrate species often inhabit the same environment as adults where the two groups potentially compete for resources and experience the same potential predators (Werner & Gilliam 1984). The smaller size of juveniles may make them vulnerable to a larger suite of potential predators than adults and may limit the size range of prey that may be consumed, reducing competitive ability compared to adults (Schmidt-Nielsen 1985, La Barbera 1989). Such factors suggest that natural selection on performance traits affecting predator avoidance and foraging may be stronger on juveniles than adults (Carrier 1996). Studies comparing locomotor performance in nature between adults and juveniles support this hypothesis. Juvenile *Anolis lineatopis* lizards and sub-adult*Crotaphytus collaris* lizards run slower than adults, but they utilize a higher percentage of maximal sprint speed capacity than adults when escaping predators (Irschick 2000, Irschick et al. 2000, Husak 2005).

I examined how well morphological and performance traits predicted survival in hatchling and adult collared lizards (*Crotaphytus collaris*), a broadly distributed species in the southwestern United States. Collared lizards use sit-and-wait foraging to feed opportunistically on available arthropods and small vertebrates (Blair and Blair 1941, Husak and McCoy 2000, Cooper et al. 2001). Therefore, predator escape and prey capture may be contexts in which maximal sprint speed is subjected to selection. I tested whether body size and condition, hindlimb length, or maximal sprint speed capacity predicted survival, and whether there were differences in what trait(s) predicted survival between the two age classes.

Materials and methods

GENERAL METHODS

The study site was a 2-ha area on Sooner Lake dam in Pawnee County, Oklahoma where the substrate consisted of concrete-covered rip-rap boulders. In April – May 2003, adult (≥ 2 yr of age) and yearling (~ 1 yr of age) male and female lizards were captured by noosing and permanently marked with toe-clips and a unique pattern of colored paint spots for visual identification at a distance (after Baird, Acree & Sloan 1996). Individuals that were captured and marked the previous year as hatchlings were considered yearlings, whereas those captured the previous year before hatchlings emerged were considered ≥ 2 yr of age. I examined survival for 54 adult lizards (12 yearling females, 14 yearling males, 15 females $\underline{\geq}$ 2 yrs old, and 13 males $\underline{\geq}$ 2 yrs old). In August – October 2003, hatchlings were captured and marked as described above. Morphological traits potentially related to survival were measured, including snout-vent length (SVL), body mass, and hindlimb length. To remove effects of body size, log-

transformed hindlimb length was regressed against log-transformed SVL, and residuals were used in subsequent analyses. The residuals from a regression of log-transformed mass against log-transformed SVL was used as an index of body condition.

MAXIMAL SPRINT SPEED

Lizards were transported to Oklahoma State University and held for one day to allow passage of gut contents. No gravid females were used. On the mornings of their second and third days of captivity, I placed lizards individually in net bags inside a lighted incubator at 37°C. Three times a day, with trials separated by at least two hours, each lizard was removed from the incubator and immediately chased down a 3-m racetrack into a black bag. The racetrack had a high-friction sandpaper substrate. I video taped runs on Hi8 film (following Braña 2003), and later viewed the tapes and counted number of frames required to traverse 1-m intervals (yearlings and adults) or 0.5-m intervals (hatchlings). The resulting speeds were comparable to those found by Peterson and Husak (in review) using a racetrack with infrared beams. I classified the quality of each run as "good" or "poor" (van Berkum and Tsuji 1987), and data from "poor" runs (pauses, reversals) were discarded. Only the single fastest 1-m or 0.5-m split for each run was analyzed. Immediately following a run, I measured the lizard's body temperature with a quick-read cloacal thermometer. All lizards were released at their exact point of capture after all trials were completed. The best and second-best performances of each individual, regardless of the day on which they occurred, were highly correlated, indicating high repeatability for adults ($r = 0.95$, $p < 0.001$) and hatchlings ($r = 0.90$, $p < 0.001$). To remove the effects of body size, log-transformed sprint speed was regressed against log-transformed SVL, and residuals were used in subsequent analyses.

SURVIVAL

I determined survival in the field to the beginning of the next activity season. The time between release and assessment of survival encompassed two ecologically important times during which lizards may have perished. The first was during the activity season when predation, starvation, or injuries associated with intra- or inter-specific interactions may have caused death. The second was a period of over-wintering when the lizards are quiescent and when mortality may have resulted from freezing, predation, infection, or insufficient energy stores. This approximately spanned mid-August – late-March for adults and late-October – late-March for hatchlings. My goal was to determine what trait(s) best predicted survival over these entire time periods, not to predict survival during one or the other of the two ecological periods. Hence, my estimate of condition has limited utility for how well it can accurately predict survival, especially for the later over-wintering period (see Discussion). Body condition of lizards, especially territorial males, decreases over the activity season (e.g., Abell 2000), so my measure of condition early in the season may be important to survival up to over-wintering, but it might not reflect winter survival. To test this hypothesis specifically, one would need to measure condition just prior to lizards over -wintering, and after they have presumably increased body fat stores after activities associated with reproduction are completed (e.g., territorial patrol in males and egg production in females). Despite these limitations, I made predictions based on the data available. If most deaths were due to starvation (i.e., insufficient energy stores during the active season or over-winter), I predicted that body condition or body size would best predict survival and sprint speed would be non-

significant, whereas if selection pressures associated with activity were the primary cause of death, I predicted that sprint speed or body size would best predict survival.

ANALYSIS

I first used two-tailed t-tests to examine differences in traits between survivors and non-survivors, analyzing hatchlings and adults separately. I used logistic regression (e.g., Janzen & Stern 1998) to test for both directional (linear) and stabilizing (quadratic) selection (Lande & Arnold 1983). All independent variables were $\log_{10}$-transformed for analysis. The dependent variable was the untransformed probability of survival (i.e., 0 or 1). Separate logistic regressions were conducted for hatchlings and adults. The linear selection logistic regression model included SVL, residual hindlimb length, body condition, residual sprint speed and sex (male = 1, female = 0). In adult analyses, age (adult or yearling) was included as a variable. The results were qualitatively the same if body mass was included in the analysis instead of body condition. The quadratic selection logistic regression model included squared residual hindlimb length and squared residual sprint speed. The results for the residuals were qualitatively similar to those obtained for absolute hindlimb length and sprint speed. Where significant logistic regression models were obtained, the methods of Janzen & Stern (1998) were used to convert the standardized (i.e., multiplied by the pre-selection standard deviation of the trait, σ_z) logistic regression coefficients into selection coefficients, using the average gradient of the estimated selection surface (i.e., the probabilities of survival). This results in selection coefficients ($\beta_{avggrad}$) comparable to those obtained from multiple linear regression (Janzen & Stern 1998). All analyses were conducted in S-Plus v. 6.1 (Insightful Corporation, Seattle. WA, USA).

Results

Of 54 adult lizards marked in 2003, 24 (44%) survived to 2004. Survivors and non-survivors did not significantly differ in SVL ($t = 0.05$, d.f. = 52, $p = 0.96$, Table 1), residual hindlimb length ($t = -0.44$, d.f. = 52, $p = 0.66$, Table 1), body condition ($t = 0.56$, d.f. = 52, $p = 0.58$, Table 1), or residual sprint speed ($t = -0.49$, d.f. = 52, $p = 0.63$, Table 1). The results are qualitatively the same if yearlings and adult lizards are analyzed separately and if males and females are analyzed separately. Of 64 hatchling lizards marked in 2003, 31 (48%) survived to 2004. Survivors and non-survivors did not differ significantly in SVL ($t = -1.30$, d.f. = 62, $p = 0.20$, Table 1) or body condition ($t = 1.06$, d.f. = 62, $p = 0.30$, Table 1). However, survivors had significantly larger hindlimb residuals ($t = -2.62$, d.f. = 62, $p = 0.01$, Table 1) and significantly larger sprint speed residuals ($t = -8.41$, d.f. = 62, $p < 0.001$, Table 1) than non-survivors.

The linear selection logistic regression model for adults was not significant ($\chi^2 = 5.85$, d.f. = 6, $p = 0.44$), nor were any partial regression coefficients. Likewise, the quadratic selection logistic regression model for adults also was not significant ($\chi^2 = 7.20$, d.f. = 8, $p = 0.52$). The results are qualitatively the same if yearlings and adult lizards are analyzed separately. The linear selection logistic regression model for hatchlings was significant ($\chi^2 = 13.00$, d.f. = 5, $p = 0.02$) with only residual sprint speed significantly predicting survival (Table 2). This indicates directional selection on residual sprint speed in hatchlings but not adults. The quadratic selection logistic regression model for hatchlings was not significant ($\chi^2 = 10.80$, d.f. = 7, $p = 0.15$).

Discussion

This study revealed a positive relationship between locomotor performance and

survival in hatchling but not adult lizards. This is consistent with the hypothesis that juveniles are likely under stronger selective pressure from predators and/or for foraging proficiency than adults. This could reflect a minimum range of speeds that individuals must attain for success in escaping predators and/or foraging. Correspondingly, the maximal sprint speed capacity of non-surviving hatchlings barely lies within the range of that measured for older age classes while foraging and escaping predators (Husak 2005). Yearlings and adults run on average between 0.8 and 1.3 m/s while foraging and 2.0 and 2.5 m/s while escaping predators (Husak 2005). Given these, it is unlikely that non-surviving hatchlings were unsuccessful at foraging since the maximal capacity of hatchling survivors and non-survivors (Table 1) was well above the average speeds used by older lizards. However, the average maximal speed of hatchling non-survivors was approximately equal to that used by older lizards while escaping predators in nature. Average maximal capacity of hatchling survivors was greater than what is used by older lizards while escaping predators. This suggests two possibilities for how maximal sprint speed may be under directional selective pressure from predators.

First, hatchling non-survivors simply may have been unable to attain speeds sufficient to escape predators. The primary predators of collared lizards are snakes and raptorial birds (Husak et al. in review), and hatchling collared lizards are likely vulnerable to a larger size range of snake predators compared to yearlings and adults. While modifying escape behaviour may be sufficient to compensate for poor locomotor performance in some instances (Husak 2005), if snake predators can approach close to hatchlings, then fast sprint speeds may be necessary for escape. The second way that sprint speed performance may be under selective pressure is indirect. Lizards might

compensate for low maximal capacity by using escape speeds closer to maximal capacity (Irschick et al. 2000, Irschick 2002, Husak 2005). Frequent use of near maximal capacity may cause elevated levels of corticosterone or high expenditures of energy, both of which can reduce survivorship (e.g., Brown et al. 2005; Civantos & Forsman 2000). However, the consequences of using near-maximal capacity often are poorly understood and deserve further empirical attention.

Arnold's (1983) paradigm predicts a correlation between variation in fitness-related performance and variation in relevant morphological traits. For collared lizards, hindlimb length was positively correlated with sprint speed in hatchlings ($r = 0.28$, $p = 0.026$), but not in yearlings and adults ($r = 0.12$, $p = 0.39$). Correspondingly, survival was predicted by sprint speed in hatchlings but not adults. It would be instructive for future research to examine what determines sprint speed within these specific age classes. Muscle cross-sectional area or muscle fiber composition are possibilities (e.g., Bonine & Garland 1999). Variation in hindlimb length of hatchlings seems at least partially responsible for variation in sprint speed, indicating that selection on sprint speed influences the evolution of limb length in collared lizards. It is worth noting that the logistic regression analyses revealed that residual sprint speed, but not residual hindlimb length, predicted survival of hatchlings, yet t-tests revealed that both residual sprint speed and residual hindlimb length differed between survivors and non-survivors. These results emphasize the relatively more important role of whole-animal performance compared to morphological traits that underlie that performance in determining fitness.

Body condition did not significantly predict survival in either hatchlings or adults, but this result does not mean that body condition is unimportant to survival. My goal was

to determine what traits, as measured at a discrete point in time, would predict survival in different age groups of lizards. Hence, I measured condition at the same time as the other traits measured, at the peak of the active season. Condition very likely changes over the course of the activity season (Abell 2000) when sexually mature lizards are involved in reproductive activities. If condition deteriorates during the season (Abell 2000) and then improves at the end of the season after reproduction has ceased, then my measure of condition may not be predictive of over-winter survival. However, condition as I measured it may be important during the time period from measurement to over-wintering. To accurately determine how well condition might influence survival, one could take multiple measurements over the activity season. To determine how well fat stores influence over -winter survival one could measure condition as close to over -wintering as possible and determine survival to the beginning of the next activity season. The utility and validity of body condition indices have been the subject of controversy (e.g., Green 2001; but see Schulte-Hostedde et al. 2005), so I cautiously interpret the significance (or the lack thereof) of my results relative to body condition and survival. Investigators studying the evolution of phenotypic traits should clearly define what body condition indices mean and what their limitations are in studies of survival and selection.

Maximal locomotor capacity in lizards has been proposed to be under selective pressures related to predation and foraging proficiency (Christian and Tracy 1981, Webb 1986, Irschick and Losos 1998). My results suggest that predation pressure, but not foraging proficiency, is an important selective force operating on sprint speed performance of hatchling lizards, but less so in adults. The result is selection on underlying morphology that constrains performance. The finding that only linear

selection is operating on the traits measured, and not quadratic selection, suggests that there is directional selection on performance and its underlying morphological basis.

The lack of a performance-fitness relationship in yearlings and adults raises some questions. Is performance of these older age classes under the influence of some other selective pressure(s)? If so, does the most important pressure differ between the sexes? Adult collared lizards are sexually dimorphic in relative hindlimb length (McCoy et al. 1994), with the development of sexual dimorphism beginning at sexual maturity. Previous work has shown that territorial adult males likely face strong sexual selection pressures to be fast for purposes of territory defence, whereas sprint speed of yearlings and adult females may be under selection for predator avoidance (Husak 2005). These results, together with the present study, suggest a complex scenario in which there are differing selective pressures operating at different intensities through ontogeny and between the sexes. Future work will reveal how general these ontogenetic and sexual differences in selection are among taxa and their ultimate effects on phenotypic expression.

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Table 1. Descriptive statistics (mean ± 1 SEM) for surviving and non-surviving hatchling and adult collared lizards (*Crotaphytus collaris*). Numbers in parentheses represent the number of individuals for that category. Bold values represent a significant difference in residual values between survivors and non-survivors using t-tests (see text).

	Hatchlings		Adults	
	Survivors (31)	Non-survivors (33)	Survivors (24)	Non-survivors (30)
SVL	66.25 ± 1.38	63.53 ± 1.80	93.06 ± 1.89	93.11 ± 1.52
Hindlimb length	**54.83 ± 1.22**	**51.39 ± 1.42**	73.32 ± 1.59	73.14 ± 1.45
Mass	13.79 ± 0.97	12.83 ± 1.17	30.90 ± 2.60	30.30 ± 2.03
Condition	-0.0071 ± 0.008	0.0067 ± 0.01	-0.0086 ± 0.01	0.0027 ± 0.02
Sprint speed	**3.33 ± 0.06**	**2.50 ± 0.06**	3.34 ± 0.09	3.38 ± 0.07

Table 2. Summary of linear selection analyses (directional selection) on morphological and performance traits of hatchling collared lizards using logistic regression. Coefficients represent $\beta_{avggrad}$ (Janzen & Stern 1998). For sex, male = 1, female = 0.

	Selection Coefficient	P-value
SVL (mm)	-0.005	0.86
Residual		
hindlimb length	0.039	0.18
Condition	-0.034	0.24
Residual		
sprint speed	0.229	< 0.001
Sex	-0.035	0.20

SEXUAL SELECTION ON WHOLE ANIMAL PERFORMANCE: LIZARD LOCOMOTION AND MATING SUCCESS

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***Abstract.* –** Studies of sexual selection have focused mainly on morphological and behavioral traits, whereas studies examining the evolution of physiological and morphological traits have focused on selection acting on whole-animal performance. While most studies of performance evolution have focused on the role of natural selection via differential survival, the general approach of examining whole animal performance as the trait directly under selection (instead of morphological traits) may be applied to studies of sexual selection. I investigated the potential for sexual selection on sprint speed performance in collared lizards (*Crotaphytus collaris*), considering the influence of circulating hormone levels as alternative targets of sexual selection. Among territorial, adult male collared lizards, only sprint speed significantly predicted territory area and number of offspring sired as determined by genetic paternity analysis. Body size, head size, and hindlimb size had no effect. Neither testosterone nor corticosterone correlated with sprint speed, territory area, or number of offspring sired. Thus, my results provide a direct link between whole-animal performance and mating success, suggesting that intra-sexual selection acts directly on sprint speed performance and drives the evolution of underlying morphological traits. Behavioral traits contributing to mating

success likely interact with, or are constrained by, whole-animal performance, leading to variation in mating success within a population.

INTRODUCTION

Sexual selection often is invoked to explain the evolution of phenotypic traits, but empirical confirmation of intra- and inter-sexual selection has focused mainly on morphological and behavioral traits (Andersson 1994; Berglund et al. 1996; Hill et al. 1999). Such sexually selected traits may also be under the influence of natural selection (e.g., differential survival), leading to simultaneous selection pressures that may be parallel or opposing (Endler 1983; Ryan et al. 1982; Grether and Grey 1996). A complete test for selection should include the phenotypic trait directly affected by selection, and many authors have emphasized the importance of whole-animal performance traits, the manifestations of underlying variation in morphology and physiology (Bartholomew 1958; Huey and Stevenson 1979; Arnold 1983). In this "performance-outward" scheme, variation in morphology constrains variation in whole-animal performance, which in turn determines variation in fitness (Arnold 1983). This framework has often been applied to examine aspects of natural selection related to differential survival (Jayne and Bennett 1990; Kingsolver 1999; Le Galliard et al. 2004; Miles 2004), but, as shown in this paper, it may also be applied in studies of sexual selection.

There has been a recent interest in sexual selection as an evolutionary force operating on whole-animal performance traits. In particular, locomotor performance of lizards has been suggested to be under the influence of sexual selection, as it has been shown to predict dominance in lizards in experimental arenas (Garland et al. 1990;

Robson and Miles 2000; Perry et al. 2004). However, studies linking locomotor performance to dominance were unable to explain how being a better locomotor performer would lead to dominance. In most cases alternative hypotheses, such as indirect selection on correlated traits (e.g., testosterone), were just as plausible as the hypothesis that sexual selection was acting directly on locomotor performance. Aside from the question of whether selection was acting directly or indirectly, these studies also lacked any explanation of how locomotor performance might be connected to dominance (and presumably fitness) through variation in behavior (Garland and Losos 1994; Irschick and Garland 2001). For example, do individuals use maximal performance capacity in the context during the activity of interest (e.g., during male-male contests in this case)?

Studies of performance relevant to fighting have more completely addressed how those performance traits link to dominance. Shore crabs with stronger claws (Sneddon et al. 1999) and lizards that bit harder (Lailvaux et al. 2004) were more likely to be dominant over worse performers during staged interactions. Similarly, *Euoniticellus intermedius* beetles with greater maximal exertion capabilities had greater fighting ability than those with less exertion capabilities (Lailvaux et al. in press). Key to these latter studies is that the performance trait under investigation had an intuitive and empirically-based connection to behavior involved in male competition (e.g., intra-sexual selection).

Returning to locomotor performance, how might it be under the influence of intra-sexual selection? Its link to dominance may be indirect, but its link to territory defense in nature may be direct. Peterson and Husak (in review) found that maximal sprint speed predicted territory size better than body size in collared lizards (*Crotaphytus collaris*), suggesting that faster-sprinting individuals had the ability were able to translate higher

speeds into a greater share of the limited, suitable habitat. Subsequent studies revealed that territorial male collared lizards used near-maximal sprint speed capacity only when responding to a rival territorial male tethered at their territory boundary (Husak 2005), further indicating that sexual selection may act directly on maximal sprint speed.

My objective was to test the hypothesis that sexual selection is operating on maximal sprint speed in male collared lizards (*Crotaphytus collaris*), taking into account previous research on the use of sprint speed in nature and how sprint speed influences survival (Husak 2005), while simultaneously testing an alternative mechanistic hypothesis (e.g., correlation with circulating hormone levels). Collared lizards display sexual dimorphism in body size and head and limb size, with males being larger than females (McCoy et al. 1994). Males and females typically become sexually mature during their first year (hereafter "yearlings;" Baird et al. 1996; Baird and Timanus 1998), but males typically do not acquire and defend an exclusive territory until their second year (Baird et al. 1996). I measured maximal sprint speed and circulating testosterone and corticosterone levels to determine how well those traits explained variation in annual reproductive success relative to morphological traits. Specifically, I predicted that maximal sprint speed would positively relate to annual mating success (as estimated by territory size and the number of offspring sired). If sexual selection on sprint speed is direct, I predict circulating hormone levels to explain little variation in sprint speed and annual mating success, whereas sprint speed will explain the most variation in annual mating success. If sexual selection is indirect on sprint speed via selection on hormone levels, then I predict circulating levels of hormones to explain significant variation in

sprint speed and annual mating success, and sprint speed to explain less variation in annual mating success.

METHODS AND MATERIALS

General Methods

The study site was a 2-ha area on Sooner Lake dam in Pawnee County, Oklahoma, on a substrate consisting of concrete-covered rip-rap boulders. In 2003 and 2004 I captured adult (≥ 2 yr of age) and yearling (~ 1 yr of age) male and female lizards by noosing. Each lizard was permanently marked by toe-clipping, and each was given a unique pattern of colored paint spots for visual identification at a distance (after Baird et al. 1996). Individuals that were captured and marked the previous years as hatchlings were considered yearlings, whereas those that were marked the previous year before hatchlings emerged were considered ≥ 2 yr of age. In most cases, toes were saved in lysis buffer for genetic analysis (see below). Hatchlings emerge in late summer – early fall in this part of Oklahoma (Husak et al. 2004). I captured hatchling lizards as they emerged and processed them as above. I used surveying equipment to generate coordinates for scale maps of the site and determine home range sizes (see Husak and Fox 2003a, 2003b). The maps were scale representations of the study area with points on the maps designating numbered flags on the actual site. The flags were spaced (approximately 11 m) such that several could be seen from any given location, and accurate locations could be determined for each lizard sighting by visual triangulation. I walked the site daily during the entire breeding season (late April – late June),observed lizards with binoculars, and mapped their locations so that territories could be defined by the minimum convex polygon procedure, using at least 20 sightings per lizard (Appendix

1A). While 20 sightings may underestimate territory area (Stone and Baird 2002), I had more sightings for all territorial males (mean ± 1 SEM = 27.2 ± 0.8; range = 24 – 34). Although many of the territorial males were present in 2003 and 2004, I used each male only once in analyses in the first year for which I had complete data for that male in order to avoid pseudoreplication.

Maximal Sprint Speed

At the peak of the breeding season (late May, Baird et al. 2001) I transported lizards to Oklahoma State University and held them for one day to encourage the passage of gut contents. Snout-vent length (SVL), total hindlimb length (HL), and head width (HW, following Lappin and Husak 2005) of lizards were measured with vernier calipers to the nearest 0.1 mm. On the mornings of their second and third days of captivity, I placed lizards individually in mesh bags inside a lighted incubator set at 37°C. Three times a day (trials being separated by at least two hours), each lizard was removed from the incubator and immediately chased down a 3-m racetrack into a black bag. The racetrack had a high-friction sandpaper substrate. I video taped runs on Hi8 film, and later viewed the tapes and counted number of frames it took a lizard to traverse 1-m intervals (following Braña 2003). Speeds obtained with this method were comparable to those found by Peterson and Husak (in review), who used a racetrack with infrared beams. I classified the quality of each run as "good" or "poor" (van Berkum and Tsuji 1987), and data from "poor" runs (pauses, reversals) were discarded. Only the single fastest 1-m split for each run was analyzed. Immediately following a run, I measured the lizard's body temperature with a quick-read cloacal thermometer. After all trials were completed, I released all lizards at their exact point of capture. The best (fastest) and

second-best performances of each individual were significantly correlated, regardless of the day on which they occurred, indicating high repeatability ($r = 0.94$, $p < 0.001$).

Hormone Assays

The collection of blood samples was concurrent with a study of seasonal variation in circulating steroid hormone levels, so to avoid the potential influence of prior handling on hormone levels, I sampled males only once a season. This limited the number of lizards available for sampling during the peak of the breeding season. I collected approximately 100 µl of whole blood by puncturing the suborbital sinus with a hematocrit capillary tube. Blood was collected from lizards over the course of only four days in late May one week before sprint speed was determined (taken between 1000 – 1300 h each day). If a lizard moved more than 1 m while I attempted to capture it, I did not capture the lizard that day for blood collection. Blood was collected in less than 1.5 min after capture so as not to alter circulating hormone levels. Once a sample was collected it was transferred to a 0.75-ml microcentrifuge tube and placed on ice until it was returned, approximately $\leq$ 5 h later, to the laboratory where plasma was separated from red blood cells. Plasma samples were frozen at- 70° C until assays were conducted.

Plasma samples were thawed and mixed with 0.5 ml dH_2O to provide sufficient volume for steroid extraction. Plasma levels of testosterone (T) and corticosterone (CORT) were measured by standard radioimmunoassay (RIA) techniques following extraction and chromatographic separation (following Wingfield and Farner 1975 and modifications by Schwabl 1993; Painter et al. 2002; Lovern and Wade 2003). Plasma samples were extracted twice with diethyl ether and reconstituted in 10% ethyl acetate in isooctane. Steroids were isolated and additional neutral lipids were removed in

diatomaceous earth columns during chromatographic separations (Lovern and Wade 2003). After this, samples were dried under nitrogen gas, resuspended in phosphate buffered saline, and maintained overnight at 4° C. Competitive binding RIAs were performed using the respective tritiated steroid tracer (for T or CORT) and antisera from Wien Laboratories for T and Sigma for CORT. Prior to conducting assays on samples for this study, parallelism was confirmed for both steroids using extra samples collected from lizards not involved in this study. The standard curves for both hormones ranged from 1.95 to 500 pg and were run in duplicate. Samples were run in duplicate, averaged, and adjusted for individual recovery and initial sample volume. The intra-assay coefficient of variation (CV) was 5.6 % for T and 4.2 % for CORT.

Paternity Assignment

Blood or toes were collected from as many potentially reproducing individuals (> 95%) and hatchlings as possible. Genomic DNA was extracted from approximately 50 µl of whole blood or two phalanges following the method of Longmire et al. (1997). Before the extraction process, toes were removed from lysis buffer, smashed with the end of a sterile syringe, and returned to fresh lysis buffer. The same extraction procedure was used for toes and blood, except toes were left incubating with proteinase K at 37° C for 24 hr longer. I amplified 10 microsatellite loci using the polymerase chain reaction (PCR) with previously published primers developed by Hutchison et al. (2004). Primers were redesigned to allow multiplex gel loading, and annealing temperatures were adjusted to allow optimization of PCR product (Table 1).

I conducted PCR amplifications in 15-µl volumes containing 1.2 µl genomic DNA, 0.5 µl of each primer, 3.8 µl double distilled H_2O, and 9 µl True Allele Premix

(Perkin-Elmer Applied Biosystems, Foster City, CA). The thermal profile consisted of a denaturation and enzyme activation cycle at 95° C (12 min); and 30 cycles of 95° C (30 s) denaturation, 46-58° C (30 s) annealing (temperature depended on locus, Table 1), and a 72° C (30 sec) elongation. I used a final 72° C (2 min) incubation to ensure that all reactions had gone to completion. I used an automated DNA sequencer (model 377, Perkin-Elmer Biosystems, Foster City, CA) to visualize variation at individual microsatellite loci. Amplicons for each locus (never more than 4 loci per lane) from a single individual were mixed (1.5 µl PCR product) and 1.5 µl of this mixture was combined with 3.5 µl of loading mixture (2.5 µl formamide, 0.5 µl ROX size standard, 0.5 µl loading dye). The PCR-loading dye mixture was denatured at 95° C for 5 min and 1.5 µl was loaded into a single lane of a 5% polyacrylamide gel. Genotypes were visualized using GENESCAN and Genotyper software (Perkin-Elmer Biosystems, Foster City, CA).

I tested for deviations from Hardy-Weinberg equilibrium using ARLEQUIN (Schneider et al. 2000), and I examined genotypic data for the presence of null alleles using Micro-Checker (University of Hull, Hull, UK). I then used Doh! (Paetkau et al. 1995; Brzustowski 2002) to determine the probability of identity and CERVUS 2.0 (Marshall et al. 1998) to assign parents to hatchling lizards at 80% confidence (Coltman et al. 1998; Marshall et al. 1998). Three loci showed relatively high frequencies of null alleles. One locus (Orig11; null allele frequency = 0.101) was not very polymorphic, so it was removed from analysis. The other two (Orig7, N5; null allele frequencies = 0.142 and 0.098) were highly polymorphic, making them desirable to include in the analyses. To prevent false exclusion, all offspring which were found to be homozygotes at either of

these two loci were entered as typed at only one allele (following LeBas 2001). This prevents offspring that are carrying their parent's null allele from being mismatched from their true parent. Only males were included as potential parents.

Statistical Analysis

Hormone levels did not significantly differ between 2003 and 2004 (T: $t_{12} = 0.64$, $p = 0.48$; CORT: $t_{9.8} = 1.24$, $p = 0.25$), so these two years were pooled for analyses. Because the number of individuals obtained for hormone assays was limited (14 of the 19 lizards used in the analyses described below), I first looked for correlations between circulating T or CORT levels and sprint speed and annual reproductive success. If any of the correlations were significant, I included hormone levels in subsequent analyses.

To evaluate the power of body size and morphology versus sprint speed in predicting territory area and number of offspring sired, I performed two correlation analyses. First, I calculated Pearson product-moment correlations between absolute measures and estimates of annual fitness. Second, I calculated correlations using residuals from (log-transformed) measurements regressed on (log-transformed) body size to examine the relationship between size-adjusted performance and the estimates of fitness. I then used multiple regression to determine what best predicted either territory size or number of offspring sired, including body size (SVL), head width, maximal sprint speed, hindlimb length, and hormone levels (if necessary) as independent variables. Morphological and performance data were log transformed before analysis. The two dependent variables (territory area and number of offspring sired) were each subjected to a separate multiple regression model. I assessed multicolinearity with the Durbin Watson (D-W) statistic (Neter et al. 1996).

RESULTS

Territory areas (mean = 1727.8 m^2; S.E. = 201.4) spanned a large range of values (431 - 2587 m^2). Of 154 offspring in the two years, 146 were assigned a sire with at least 80% confidence. Of those 146, 68 (47%) were assigned to territorial males for which I had data on sprint speed and territory area. The remaining offspring were assigned to the same male in a different year (44, 30%), other territorial males for which I did not have a complete dataset (9, 6%), and yearling males (25, 17%). Of the males for which I had a complete dataset, the number of offspring sired ranged from one to ten (mean = 3.6; S.E. = 0.6). The number of offspring sired was significantly and positively correlated with territory area ($r = 0.55$, $p = 0.02$).

Testosterone levels did not correlate with sprint speed ($r = 0.004$, $p = 0.85$), territory area ($r = -0.49$, $p = 0.13$), or number of offspring sired ($r = 0.045$, $p = 0.90$). Corticosterone levels also did not correlate with sprint speed ($r = 0.19$, $p = 0.13$), territory area ($r = 0.033$, $p = 0.92$), or number of offspring sired ($r = 0.35$, $p = 0.29$). Thus, circulating hormone levels were not included in multiple regressions.

Sprint speed was significantly and positively correlated with territory area ($r = 0.68$, $N = 18$, $p = 0.002$; Figure 1A) and number of offspring sired ($r = 0.69$, $N = 19$, $p = 0.001$; Figure 1B). Body size (SVL) was not correlated with territory area ($r = 0.45$, $N = 18$, $p = 0.06$; Figure 2A) or number of offspring sired ($r = 0.04$, $N = 19$, $p = 0.88$; Figure 2B). Hindlimb length was not significantly correlated with territory area ($r = 0.40$, $N = 18$, $p = 0.10$), but it was positively correlated with number of offspring sired ($r = 0.47$, $N = 19$, $p = 0.04$). Head width was not correlated with territory area ($r = 0.41$, $N = 18$, $p = 0.09$) or with number of offspring sired ($r = 0.33$, $N = 19$, $p = 0.17$). Size-corrected sprint

speed was significantly and positively correlated with territory area and number of offspring sired ($r = 0.55$, $N = 18$, $p = 0.02$; $r = 0.74$, $N = 19$, $p < 0.001$, respectively). Size-corrected hindlimb length was not correlated with territory area ($r = 0.14$, $N = 18$, $p = 0.59$), but it was positively correlated with number of offspring sired ($r = 0.60$, $N = 19$, $p = 0.007$).

Multiple regression with territory area as the dependent variable produced a significant model ($F_{4, 13} = 4.35$, $p = 0.019$, D-W = 2.147). A significant model also was generated with number of offspring sired as the dependent variable ($F_{4, 14} = 5.00$, $p = 0.010$, D-W = 1.77). All models showed little multicolinearity. Sprint speed was the only significant predictor of territory area ($\beta = 0.83$, $p = 0.006$) and number of offspring sired ($\beta = 0.64$, $p = 0.018$). Using residual sprint speed and residual hindlimb length values (calculated by regressing the log-transformed variable on log-SVL) in the model instead of absolute values resulted in qualitatively similar results. With the removal of sprint speed as an independent variable, the multiple-regression model with territory area as the dependent variable lost statistical significance ($p = 0.30$), whereas the multiple-regression model with number of offspring sired as the dependent variable was marginally nonsignificant ($p = 0.064$). In the latter model only hindlimb length approached statistical significance ($p = 0.058$; all other variables $p > 0.08$).

DISCUSSION

I found that only sprint speed predicted territory size and annual mating success in territorial male collared lizards, whereas measures of body size, head size, limb size, and circulating hormone levels did not. These results link variation in maximal sprint speed to a component of fitness (annual male mating success) and demonstrate the importance

of intra-sexual selection in the evolution of whole-animal performance. Faster territorial males had higher mating success than slower territorial males. Previous studies have focused on linking performance with estimates of survival (see Introduction), leaving unexplored the possibility of sexual selection as an important factor in the evolution of whole-animal performance.

Whole-animal performance traits are integrated manifestations of underlying morphological and physiological traits, leading to the prediction that variation in the latter traits should predict variation in performance. Residual hindlimb length was positively correlated with residual sprint speed in territorial males ($r = 0.63$, $p = 0.004$), suggesting that selection on sprint speed may be an important selective force in the evolution of hindlimb length in collared lizards. This is consistent with the observed sexual dimorphism in hindlimb length in collared lizards where males have relatively longer limbs than females (McCoy et al. 1994). The remaining unexplained variation in sprint speed is likely due to other traits such as muscle cross-sectional area or fiber composition (e.g., Bonine et al. 2001). Body size was not a significant predictor of annual mating success, and it was not significantly correlated with sprint speed ($r = 0.39$, $p = 0.10$), suggesting that, for similarly sized territorial males, sprint speed is more important than body size (see also Lappin and Husak 2005). The lack of a body size effect on fitness agrees with results for another population of collared lizards (Baird et al. 2003) and with results found in another lizard species, *Sceloporus virgatus* (Abell 1997).

A correlation between sprint speed capacity and mating success is, by definition, sexual selection for sprinting capacity, but the causal selection pressures may be direct or indirect (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987). Annual mating success

may be related to sprint speed indirectly via confounding phenotypic or genetic correlations between sprint speed and overall health and vigor or behavioral motivation (Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004). In this situation, maximal sprint speed capacity of collared lizards would be a condition-dependent trait (Schluter et al. 1991; Clobert et al. 2000; Jennions et al. 2001), and selection on sprinting would not necessarily result in an evolutionary (genetic) response (Arnold 1983; Lande and Arnold 1983; Garland and Losos 1994). However, maximal sprint speed has been found to be heritable in the broad sense in several lizard species (Garland 1988; Tsuji et al. 1989; Bennett and Huey 1990; Warner and Andrews 2002; but see Sorci et al. 1995).

Alternatively, sprint speed may be correlated with circulating hormone levels (e.g., Garland et al. 1990; Robson and Miles 2000), which may be under direct sexual selection pressures for other reasons (see below). Previous studies showing a positive correlation between locomotor performance and laboratory-determined dominance have suggested that the link may be due to correlational selection on circulating testosterone levels, which are known to affect sprint speed performance (Klukowski et al. 1998). I found no correlation between circulating levels of testosterone and either maximal sprint speed or annual mating success, despite observations that experimentally elevated levels of testosterone cause increased aggression (Moore 1986; Sinervo et al. 2000), sprint speed (Klukowski et al 1998), territory size (Fox 1983; DeNardo and Sinervo 1994), and mating success (Sinervo et al. 2000). Similarly, I found no effect of corticosterone, experimentally elevated levels of which have been shown to lead reduce sprint speed (Meylan and Clobert 2004). The lack of a significant correlation between hormone levels and performance in collared lizards may be due to a small sample size, but it may also be

interpreted as supporting the hypothesis that above (or below) some threshold level, variation in hormone levels has no biologically significant effect on sprint speed. However, the relationship between natural variation in circulating hormone levels and performance traits remains unclear (Perry et al. 2004; Lappin and Husak 2005).

Sexual selection on sprint speed could be direct if speed contributes directly to effective defense of a territory with the result of excluding other males and reducing their relative fitness (Snell et al. 1988; Pough 1989). When studying the evolution of morphological and physiological traits, the most common research design is the general paradigm of testing for a significant relationship between whole-animal performance and some measure of fitness (e.g., Huey and Stevenson 1979; Arnold 1983). However, since the inception of the morphology-performance-fitness paradigm (Arnold 1983), many have proposed that behavior acts as a filter between performance and fitness, such that examination of how and when organisms utilize a performance trait can lead to powerful conclusions concerning what selective pressures are operating (Garland and Losos 1994; Irschick and Garland 2001; Irschick 2003).

Many authors have commented on the tendency of territorial male collared lizards to sprint toward rivals during intra-sexual encounters (Yedlin and Ferguson 1973; Baird et al. 2003; Peterson and Husak in review). Concurrent research (Husak 2005) on the population of collared lizards studied here revealed that territorial male collared lizards used speeds closer to maximal sprint speed capacity (90% of maximal capacity) when responding to a rival territorial male that was tethered at the boundary of their territory than when escaping predators (68%) or when foraging (31%). Further, despite large variation in maximal sprint speed capacity among territorial males (e.g., Figure 1), all

(even the inherently better performers) used near-maximal capacity when responding to a rival, whereas better performers used less of their near-maximal capacity than poorer performers in the other two contexts (Husak 2005). The use of sprint speed during intra-sexual encounters, combined with the results that sprint speed significantly predicted territory size and annual mating success suggests that sprint speed is under the direct influence of intra-sexual selection.

If sexual selection favors faster sprint speed, how might natural selection via differential survival influence it? It is likely that natural selection pressures parallel those of sexual selection in territorial males. Territorial males utilize a greater proportion of their maximal capacity when responding to rivals compared to when escaping predators and foraging (Husak 2005), but the proportion of maximal capacity used when escaping predators is still high relative to values found in other species (Irschick 2000a, 2000b, 2003). However, a study testing for a link between sprint speed and survival failed to find such a relationship in adult collared lizards (Husak 2005), suggesting that selection on sprint speed for predator avoidance is not strong. A performance-survival link was found for hatchling collared lizards (Husak 2005), however, revealing that selection for effective predator escape may be intense during early ontogeny.

I found that sprint speed was the only significant predictor of annual mating success of the traits that I measured, but other traits also have been proposed to explain variation in mating success of territorial male collared lizards. Indeed, these other traits may explain the remaining variation in mating success unexplained by the variables I measured. Lappin and Husak (2005) found that bite-force performance predicted estimates of annual mating success better than body size and measurements of the

morphology that supposedly underlie bite force (i.e., head shape). Their results are intuitively easy to reconcile with the results of my study. It is likely that multiple factors are under the influence of sexual selection in collared lizards, but via different specific mechanisms (e.g., Lande and Arnold 1983; Andersson 1994). Lappin and Husak (2005) suggested that biting and bite-force performance are important during male fights and for early spatial sorting, whereas I argue that sprint speed is important for territory defense after territories are already established. Collared lizard males in central Oklahoma typically maintain the same territories for repeated years (Baird et al. 2001), suggesting that there is strong selective pressure to be able to effectively patrol an area in a territorial neighborhood where space is very limited and the opportunities to acquire a different territory are infrequent (Baird et al. 2003). The importance of the results found by Lappin and Husak (2005) and in this study is that, in both studies, selection was operating at the level of whole-animal performance.

Baird et al. (2003) argued that male display attributes, and not body size or other morphological traits (i.e., static; Hill et al. 1999), were the best predictors of mating success in collared lizards. During threat and advertisement displays, collared lizards laterally compress their bodies and perform a series of push-ups (Fitch 1956; Baird et al. 2003; Husak 2004). Display rate and patrol rate (important attributes found by Baird et al. 2003) may be under correlated selection with sprint speed if there is the same underlying physiological basis (e.g., muscle fiber types). Extended displaying by lizards can cause a shift to anaerobic metabolism (Brandt 2003), thus increasing lactic acid concentrations in the body and restricting locomotor abilities, especially sprint speed, which is mostly anaerobic (Bonine et al. 2001; Kohlsdorf et al. 2004). Thus, variation in

anaerobic capacity may translate to variation in sprint speed capacity and display endurance. Those individuals with a higher maximal sprint speed capacity may be better able to tolerate reduced locomotor capacity due to extended displaying because a temporary decrease in their locomotor capacity may be less costly in terms of territory defense than to those with a low sprint speed capacity, which already have an inferior ability to defend a large territory. This predicts a positive correlation between maximal sprint speed capacity and patrol rate and display rate. Being a poor performer in any of these three traits could lead to lower fitness compared to better performers (e.g., Baird et al. 2003; this study). However, if all territorial males are always using near-maximal capacity to defend territories, then this disparity in cost may not be present. It is, however, unlikely that males always use near maximal capacity when defending their territories, because territorial neighbors reduce aggression toward each other once boundaries are established ('dear enemy' phenomenon, Fox and Baird 1992; Husak and Fox 2003b). Indeed, the frequent use of near-maximal capacity while responding to rivals may be one cost that the 'dear enemy' phenomenon reduces. Further research will determine to what extent easily modifiable behavioral traits that have been shown to predict mating success (Holmberg et al. 1989; Hill et al. 1999; Topping and Millar 1999; Kodric-Brown and Nicoletto 2001) interact with and/or are constrained by whole-animal performance traits and variation in its underlying morphological and physiological traits. I predict that in other polygynous taxa where behavioral traits significantly predict mating success, there is an underlying whole-animal performance trait that is under the direct influence of sexual selection.

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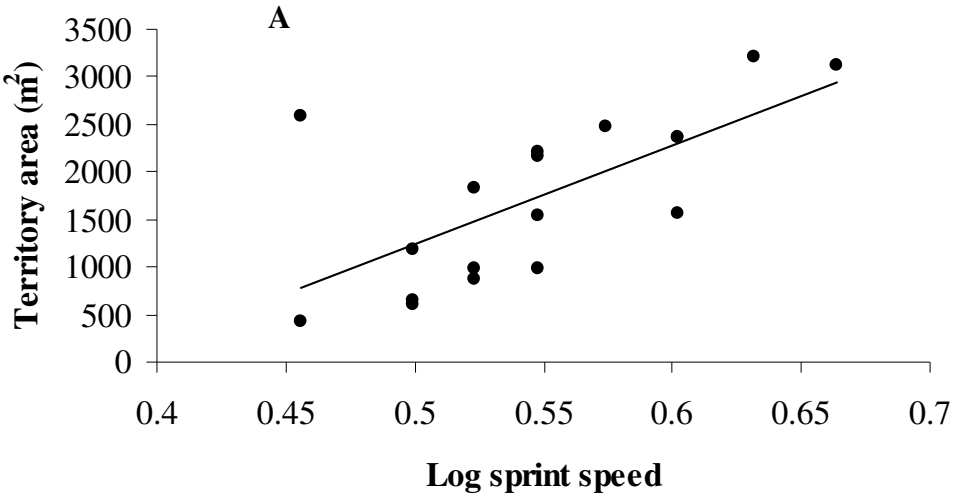
Table 1. Locus names, PCR primers, and annealing temperatures used for analysis of collared lizard (*Crotaphytus collaris*) paternity analysis. The name of each locus was originally described by Hutchison et al. (2004), but all primer sequences were modified to allow multiplex gel loading, and annealing temperatures were modified for product optimization.

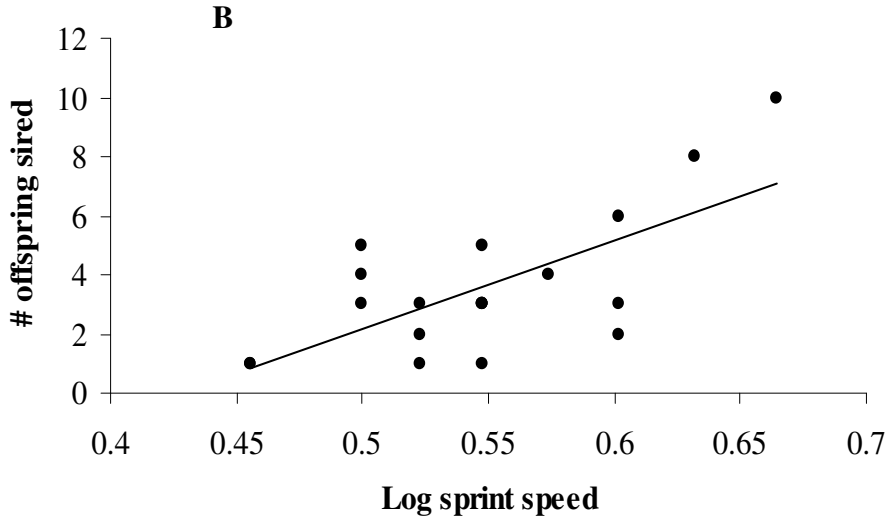
Locus	Forward Primer	Reverse primer	Temp (°C)
Orig6	6FAM-AGGACACAAACATTCTTATC	TCTGAGTATTCCTTGCTT	46
Orig7	6FAM-AGGTTGTGGTCTGTAGCA	GGATCTGTCCCAATAATG	51
Orig11	6FAM-CACTATAAGATGTAGCACTTGC	GGTAAGCACCAGATTGAGC	54
Orig24	HEX-AGTTGAACTCGATGCTCT	ATTGAACCCATGGTAAAG	50
Orig25	HEX-AGCCTTTACTGTGAGACCCA	TCATGAAATGAAGCAAAATTAATAATA	49
Orig26	6FAM-TATACATTCTTGAGTTCCGC	CAATGAGGGATATAAGGTGG	52
Enr3	HEX-CCTCAGCAGAAGCACCAGC	TATTGAGCAGGACAGGGAAG	58
Enr21	6FAM-AGGAAGGCTCAAAGGTTAC	ATTTCACACAGGAGGAGGAGG	58
Enr48	HEX-TTTGTTCTTATTTTACTTGCGT	AGGTATTGTGCTGTCTGAGG	48
N5	HEX-CTGCCATATCATGAAGGGTG	AATCAGCACACTGGGAAAG	52

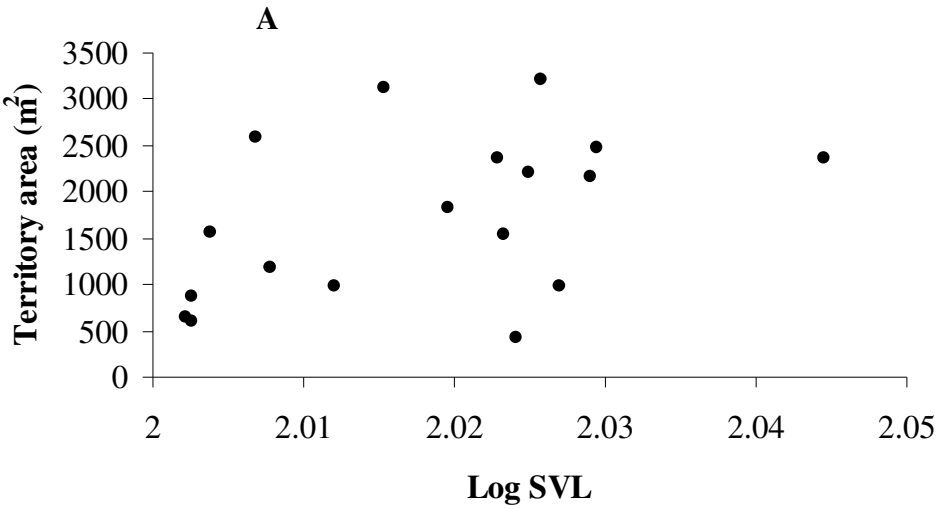
Figure Legends:

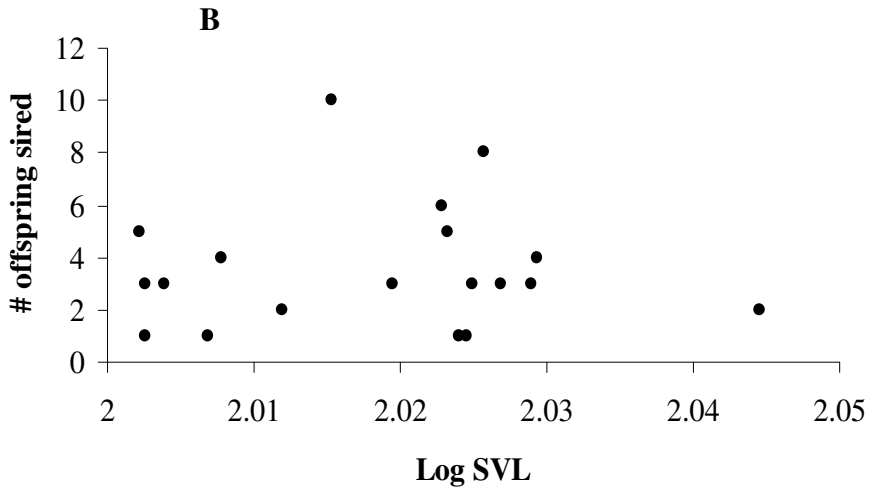
Fig. 1. Relationships between sprint speed and (A) territory size and (B) number of offspring sired in territorial male collared lizards at Sooner Lake, OK. Sprint speed was the only significant predictor of both estimates of annual fitness (see text for details).

Fig. 2. Relationships between body size (SVL) and (A) territory size and (B) number of offspring sired in territorial male collared lizards at Sooner Lake, OK. Neither of these correlations was significant (see text for details).


A
Territory area (m2)
3500
3000
2500
2000
1500
1000
500
0
0.4
0.45
0.5
0.55
0.6
0.65
0.7
Log sprint speed

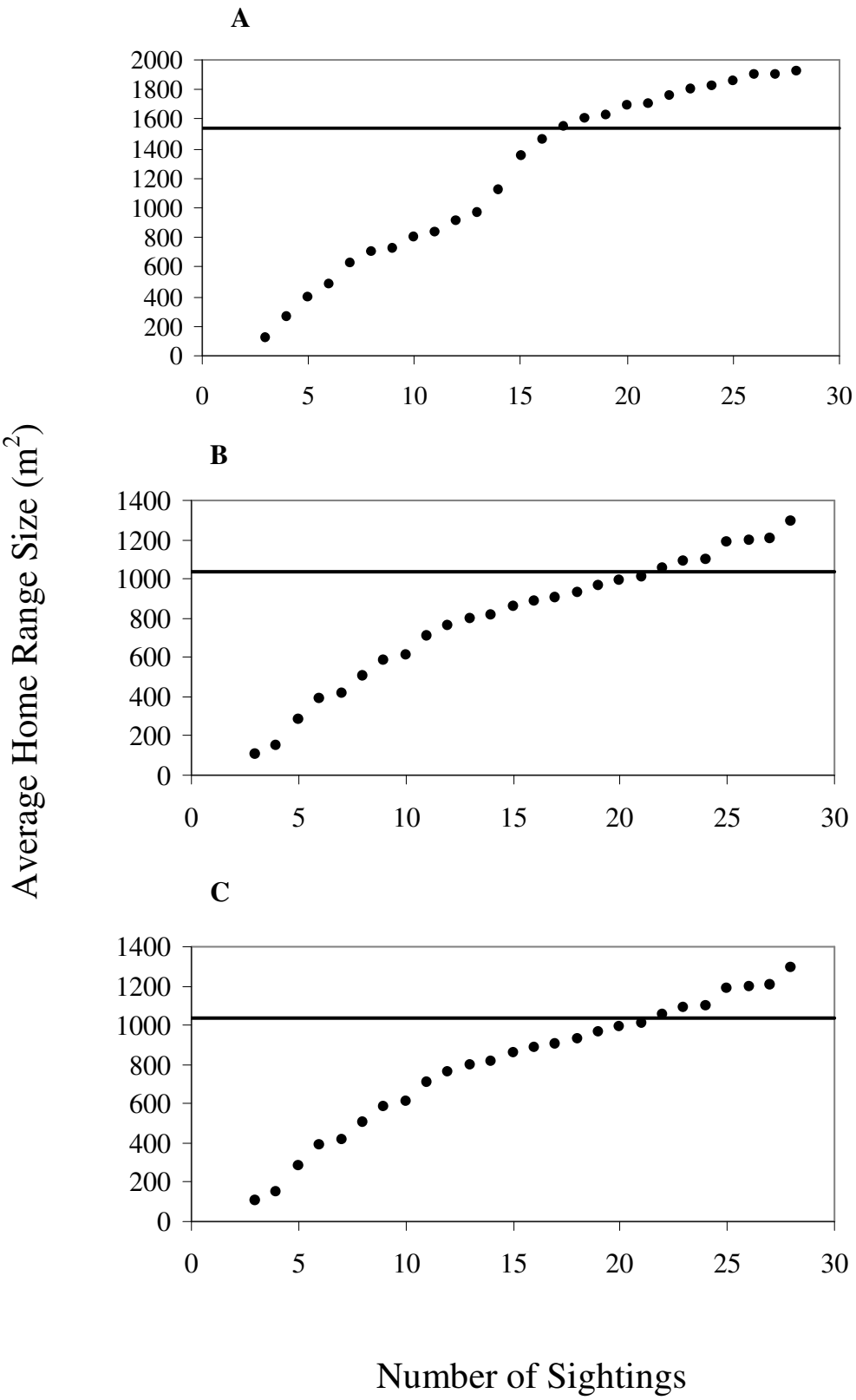

B
offspring sired
12
10
8
6
4
2
0
0.4
0.45
0.5
0.55
0.6
0.65
0.7
Log sprint speed


A
Territory area (m2)
3500
3000
2500
2000
1500
1000
500
0
2
2.01
2.02
2.03
2.04
2.05
Log SVL


B
offspring sired
12
10
8
6
4
2
0
2
2.01
2.02
2.03
2.04
2.05
Log SVL

APPENDIX

Plots of average home range size versus the number of sightings for collared lizard (*Crotaphytus collaris*) (A) territorial males (N = 14), (B) yearling males (N = 19) , and (C) females (N = 43) in 2003. The line intersecting the y-axis represents 80% of average home range size. The x-axis value when the empirical curve touches this line is the minimum number of sightings required to accurately determine home range area.


A
2000
1800
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1200
1000
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200
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30
B
1400
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200
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5
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15
20
25
30
C
1400
1200
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600
400
200
0
0
5
10
15
20
25
30
Average Home Range Size (m2)
Number of Sightings

VITA

JERRY F. HUSAK

Candidate for the Degree of

Doctor of Philosophy

Thesis: ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF LOCOMOTOR PERFORMANCE IN COLLARED LIZARDS (*CROTAPHYTUS COLLARIS*)

Major Field: Zoology

Biographical:

Personal Data: Born in Victoria, Texas on 12 December 1975, the son of Jerry J. Husak III and Genevieve H. Husak

Education: Graduated from Victoria High School, Victoria, Texas in May 1994; received Bachelor of Science degree in Biology from Angelo State University, San Angelo, Texas in May 1998; received Master of Science degree in Zoology at Oklahoma State University, Stillwater, Oklahoma in May 2001. Completed the requirements for the Doctor of Philosophy degree with a major in Zoology at Oklahoma State University in July 2005.

Experience: Teaching Assistant, Department of Zoology, Oklahoma State University, August 1998 to May 2005. Instructor, Biology of Amphibians and Reptiles, Department of Zoology, Oklahoma State University, Spring 2004.

Professional Memberships: American Society of Ichthyologists and Herpetologists, Animal Behavior Society, Herpetologist's League, Oklahoma Academy of Science, Society for Integrative and Comparative Biology, Society for the Study of Amphibians and Reptiles, Southwestern Association of Naturalists, Texas Academy of Science.

Name: Jerry F. Husak Date of Degree: July, 2005

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF LOCOMOTOR PERFORMANCE IN COLLARED LIZARDS (*CROTAPHYTUS COLLARIS*)

Pages in Study: 100 Candidate for the Degree of Doctor of Philosophy

Major Field: Zoology

Scope and Method of Study: The purpose of this study was to test hypotheses concerning the evolution of locomotor performance in collared lizards (*Crotaphytus collaris*). I investigated the roles of natural and sexual selection on locomotor performance in collared lizards by measuring maximal sprint speed in the laboratory, in addition to field-realized sprint speed for the same individuals in three different contexts: foraging, escaping a predator, and responding to a rival intruder. In addition I examined how well performance, morphology, and steroid hormone levels predicted survival and mating success in different age and sex classes.

Findings and Conclusions: Sprint speed predicted survival only in hatchlings, not adults. Of the three contexts, females used closer to maximal speed while escaping predators than in the other contexts. Adult males, on the other hand, used closer to maximal speed while responding to an unknown intruder tethered within their territory. Sprint speeds during foraging attempts were far below maximal capacity for all lizards. Collared lizards appeared to choose microhabitats near refugia such that maximal speed was not necessary to escape predators. Although natural selection for predator avoidance cannot be ruled out as a strong selective force acting on locomotor performance in collared lizards, especially in females and hatchlings, intra-sexual selection for territory maintenance may be a stronger selective agent on males. To further support the latter hypothesis, I found that only maximal sprint speed predicted mating success. These results represent the first connection of morphology, performance, behavior, and fitness for a population of animals, and suggest that sexual selection may act on whole-animal performance traits.

ADVISER'S APPROVAL: Stanley F. Fox